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THE STRUCTURE OF THE INTESTINAL HELMINTH COMMUNITIES OF LESSER SCAUP (*AYTHYA AFFINIS*)

by

JAY DEE HAIR

C

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "The structure of the intestinal helminth communities of lesser scaup (*Aythya affinis*)" submitted by Jay Dee Hair, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Effects of temporal and spatial segregation on the helminth communitities of lesser scaup (*Aythya affinis*)(30 adults; 52 ducklings), collected in central Alberta during the summers of 1973-74, were studied.

Thirty-three species of helminths (26 cestodes, 5 trematodes, 2 acanthocephalans) were recovered. Thirteen species were dominant (11 in adults; 11 in ducklings), of which 9 were common to both adults and ducklings. The helminth community was characterized by cestodes (98 percent of the total fauna), particularly hymenolepidids, which frequently had populations numbering in the thousands.

In adult scaup, there were no significant differences, by season or year, in the total numbers of helminths or in any of the measures of faunal diversity. Only 1 species was limited seasonally, but it was not replaced by another species. In ducklings, the acquisition of a helminth community was rapid and its complexity increased significantly with age of host. Two species demonstrated evidence of temporal segregation on the basis of host age. Overall, the community was comprised of a well established fauna, but features of temporal segregation were not particularly important in determining its complexity.

Spatial aspects of community structure were investigated by examining the distributions of helminths in 20 equal sections of the small intestines of individual birds. In adult scaup, the number of species were higher in the third quarter of the intestine, but other measures of faunal diversity (Shannon-Weaver function, equitability (J), Simpson's Index) had decreasing patterns along the intestine. In ducklings, all of the measures

of diversity were maximal throughout the mid-region of the intestine and low at both ends.

Each dominant helminth occupied a predictable location along the intestine, had a limited range, which for most species was correlated with its population size, and which overlapped those of other species. In ducklings, 3 species demonstrated significant directional changes in location with age of host, but by the time they were 1 month old, their locations were not significantly different than they were in adult scaup.

A quantitative measure of habitat niche overlap delineated 4 overlapping groups of species in adults and 3 groups in ducklings. Only 3 species, within 1 group in adults, demonstrated evidence of interactive segregations. The effects of their interactions on community structure were restricted to the anterior region of the intestine.

Spatial features, specifically selective segregation by each species of parasite, were the most important factors determining the complexity of the community. The intestinal helminth community of scaup is apparently a mature one, whose diversity has been established to an important extent through biotic interactions.

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I. INTRODUCTION

"Why are there so many kinds of animals?"
G.E. Hutchinson (1959)

Attempts to answer this celebrated riddle have been primarily the province of ecologists who have studied free-living animals. Their studies have amply demonstrated that species replace one another within and between habitats on three major niche (term used as defined by Whittaker *et al.* 1973) dimensions: temporal, trophic and spatial (reviewed by Schoener 1974). Parasitic organisms provide some excellent examples of niche segregation, along each of these dimensions.

Parasites frequently specialize their niches by separating in time their use of the same habitat or resource. For example, Crofton (1963) reported that the generation time of the abomasal nematode, *Trichostrongylus axei* was significantly longer than those of *Haemonchus contortus* and *Ostertagia circumcincta*. This results in a temporal segregation between the niches of *T. axei* and the later two species. Cannon (1972) showed that *Bunodera sacculata* and *Crepidostomum cooperi*, two closely related papillose allocreadiids that co-occur in the anterior region of the intestine of yellow perch (*Perca flavescens*), demonstrate a degree of temporal segregation. The incidence of *C. cooperi* is highest in midsummer while that of *B. sacculata* is highest during late spring and early fall. Similarly, MacKenzie and Gibson (1970) reported that *Cucullanus heterochrous* and *C. minutus* demonstrate a partial segregation since they both use the anterior intestine of flounders (*Platichthys flesus*), but mature at different times of the year. The data given by Bakke (1972) provides a somewhat more complex example of temporal segregation. The intraintestinal distributions of *Himasthla militaris* and *Plagiorchis laricola*, which overlap in the middle third of the intestine of gulls (*Larus canus*), are replaced during the later part of the summer by overlapping populations of *Diplostomum spathaceum* and *Microphallus similis* respectively.

Parasites also make use of a second type of temporal segregation - the use of different age classes of the same host species. Petter (1966) found that *Atractis dactyluris* infected only old tortoises (*Testudo graeca*), and did not reach high populations until the tortoises were at least 15 years old. The other characteristic species of tortoise pinworms were well established in younger hosts. Similarily, Dudzinski and Mykytowycz (1963) reported that *Graphidium strigosum* was found only in older rabbits (*Oryctolagus cuniculus*), but there was no relationship between age of host and level of infection for the other species of nematodes. Miller (1943) has shown that the cestode *Triaenophorus nodulosus* was found predominantly in pike (*Esox lucius*) less than 3 lb. in weight, whereas *T. crassus* was predominantly in larger pike. Miller (1952) also showed that temporal segregation in the use of populations of *Cyclops bicuspidatus* by the procercoids was an important part in the ecology of three species of *Triaenophorus*. In the last case, as in others involoving invertebrate intermediate hosts with rapid population turnover, the two types of temporal segregation cannot be distinguished (Holmes 1973).

Specialization for the use of different resources is another mechanism of niche segregation. Keast (1968) suggested that closely related sympatric species generally were separated by at least a 10% linear measurement (particularly in relation to food-gathering structures) and that the smaller species was a more specialized feeder. Relating this idea to parasites, Cannon (1972) reported that *C. cooperi* and *B. sacculata*, which co-occur in the anterior intestine of perch, showed size differences, notably a 10% difference in oral sucker diameter. In addition, the smaller species, *C. cooperi*, shows a more restricted microhabitat distribution. He concluded that coexisting allocreadiids of perch exhibit the same kinds of differences in food gathering structures as those reported for sympatric free-living organisms. In a more conclusive example of trophic segregation, Schad (1963) showed that pinworms of tortoises segregate their niches, in part, by differences in food habits associated with differences in oral morphology. The distributions of *Tachygonetria robusta* and *Tach. stylosa* overlap broadly in the colon of tortoises, but the former is an indiscriminate feeder on lumen contents, while the latter feeds of fine particulate matter recognizable mainly as bacteria. He also observed striking dissimilarities in oral structures

between other combinations of species of pinworms with similar patterns of distribution and concluded that it is probably that they also differ in food habits.

The above examples emphasize the importance of the specialization of oral structures as mechanisms of trophic segregation between closely related species of trematodes or nematodes. Acanthocephalans and cestodes lack comporable oral structures and are dependant upon the metabolic activity of the surface covering their bodies for the absorption of nutrients. In general, parasites that are "absorbers" obtain their nutritional requirements through the uptake of low molecular weight carbohydrates (Mettrick and Podesta 1975). Studies on the morphology of the surfaces of acanthocephalans and cestodes (reviewed by Crompton 1970 and Mettrick and Podesta 1975, respectively) indicate that within groups, their structures are similar. There are minor differences but they are not interpretable in terms of trophic adaptations for the absorption of these categories of compounds. In addition, resource segregation of acanthocephalans and cestodes may be for reasons other than obtaining energy. For example, studies have shown that habitat selection of some species of acanthocephalans and cestodes is correlated with changes in the chemical composition of their bodies during development (Goodchild and Wells 1957; Archer and Hopkins 1958; Mettrick and Cannon 1970; Uglem and Beck 1972) or in response to differences in oxidation-reduction potentials along the intestine (Mettrick and Podesta 1975). Consequently, contemporary parasitologists have not identified the important questions to ask about trophic specialization as a mechanism of the segregation of resources between closely related species of acanthocephalans or cestodes. Research on this subject would involve a study completely independent from other aspects of resource partitioning.

Spatial segregation is by far the most common mechanism of niche specialization demonstrated by parasites. It includes geographical (allopatric), host habitat (allotopic), and host segregation (allohospitalic) (Eichler 1966). In a major review on this subject, Holmes (1973) pointed out that spatial segregation also includes segregation to site within the host. Frequently this involves the segregation of related species of parasites in different parts of the digestive tract.

For example, in individual racer snakes (*Coluber constrictor*), three species of hookworms may occur: *Kalicephalus inermis coronellae* in the esophagus, *K. costatus parvus* in the anterior small intestine, and *K. p. rectophilus* in the rectum (Schad 1962). Madsen (1952) showed a similar situation with *Capillaria* in waterfowl: *C. contorta* occupied the esophagus, *C. caudinflata* the small intestine, and *C. anatis* the caeca.

In individual hosts, segregation of parasites along the length of the small intestine is common; examples are found almost wherever the precise location of parasites have been studied (reviewed extensively by Ulmer 1971, Crompton 1973 and Holmes 1973). For the most part the complexity and importance of site segregation depends on the abundance of species or individuals and/or the size of the helminths in relation to the intestine. When the helminths are small and present in relatively low numbers, they frequently segregate in non-overlapping zones (e.g., five species of cyclophyllideans in *Sorex araneus* studied by Lewis 1966; three species of cyclophyllideans in dogs, Baer 1971). When the helminths are larger, or abundant, they tend to occupy a greater portion of the intestine (e.g., *Hymenolepis diminuta* studied by Chandler 1939, Holmes 1961; *Taenia taeniaeformis* by Hutchinson 1957), and may overlap (e.g., seven species of hymenolepidids in ducks, Avery 1969; species of trichostrongyles in various ruminants, Sommerville 1963).

The overall importance of site segregation is best demonstrated in analyses of species flocks - several related species of parasites which occur in the same host individual at the same time. The best known examples are assemblages of pinworms in the colon of tortoises, studied by Petter (1962, 1966) and Schad (1963). They reported up to 15 species, mostly of the genus *Tachygonetria*, with some individual tortoises having over 50,000 pinworms. Both workers demonstrated that each species was selectively distributed along the length of the colon. Schad added another dimension to site segregation by studying the radial distributions of these nematodes. Using a unique approach, he quick-froze the colons of the tortoises in liquid air, cut them into sections of equal length, divided each section into an inner core and outer ring of approximately volume, and examined them for the distributions of pinworms. He reported two series

of pinworms, one equally divided between the ring and the core of the colon and one found almost entirely in the ring. Pairs of species with the most similar linear distributions differed in radial distribution and as mentioned previously, those species that overlapped broadly showed different oral structures, correlated with different food habits.

In a review on the importance of niche specialization of helminths, particularly selective site segregation, Holmes (1973) hypothesized that parasites respond to the regular presence of competition in essentially the same ways as free-living organisms, and that differential habitat selection was fundamental to the development of complex helminth communities. To test this hypothesis I initiated a research program to study the importance of niche specialization in the structure of a complex helminth community. The selection of a complex host-parasite system was based on the data provided by Graham's (1966) study of the parasites of lesser scaup (*Aythya affinis*) collected from lakes near Edmonton, Alberta. He reported over 25 species of intestinal helminths, the majority of which were cestodes (particularly hymenolepidids), which frequently had individuals numbering in the thousands.

For purposes of statistical analysis, I used the intestinal parasites from individual lesser scaup as a replicate of a complex helminth community. This approach emphasizes the importance of spatial segregation in the structure of the helminth community at the level of the host individual, as opposed to that at the level of the host population.

My major research objectives were to determine the modes and extent of the temporal and spatial aspects of niche specialization in the structure of a complex parasite community. Since cestodes characterized the community, and for the reasons mentioned previously, the role of trophic niche specialization was considered indirectly by a process of elimination.

II. GENERAL METHODS

The Study Lakes

Field collections were made at Cooking and Hastings Lakes located approximately 32 kilometers southeast of Edmonton, Alberta. Both lakes are relatively shallow, highly productive and eutrophic. Their general limnology was described by Kerekes (1965).

The invertebrate faunas of the two lakes are basically the same; the most abundant macrofaunal groups include amphipods, corixids, chironomids and other insect larvae, leeches, oligochaetes, cladocerans, copepods and ostracods. In Cooking Lake the vertebrate fauna is almost totally comprised of migratory aquatic birds, which utilize the lake for breeding and/or as a staging area for migration. Among the more important are mallards (*Anas platyrhynchos*), shovelers (*A. clypeata*), blue-winged teal (A. *discors*), lesser scaup (*Aythya affinis*), white-winged scoters (*Melanitta deglandi*), eared grebes (*Podiceps caspicus*), and Franklin's and Bonaparte's gulls (*Larus pipixcan* and *L. philadelphia*). There are no fish in this lake and very few muskrats (*Ondatra zibethica*) or beavers (*Castor canadensis*) have been sighted. The aquatic bird populations of Hastings Lake are similar to Cooking Lake except that red necked grebes (*P. grisegena*) are more abundant. Also, this lake has significant numbers of muskrats and beavers. Other details on vegetation etc. are summarized in Bethel (1972).

Field Collections and Laboratory Procedures

Many ecological studies have to be conducted within arbitrary limits set by the investigator. Based on my application of the following

procedures, I imposed both temporal and spatial limits on the data collected during my study. These limits were necessary to standardize the comparisons within and between birds. Future investigators should recognize these limitations when comparing their data with the results that I obtained.

During the summers of 1973 and 1974, equal sample sizes (5) of adult scaup were collected by shooting during the early parts of the months of June, July and August. All of the ducklings were collected in late July of each year and were placed into age-weight categories following Sugden (1973). An additional 18 scaup, collected in 1972 were used in a preliminary analysis (Hair and Holmes 1975). Due to differences in season of collection and/or methods of handling, these scaup were not readily comparable to those from 1973-74 and will not be considered in this thesis.

To prohibit post-mortem migration of the helminths, intestinal tracts were removed from the birds immediately upon collection, placed in a metal pan and frozen rapidly by adding a solution of absolute ethyl alcohol and dry-ice (at approximately -70 C). They were then removed to a container of dry-ice and kept frozen until examined.

While still frozen the small intestines (pylorus to ileo-caecal juncture) were measured then cut into 20 equal sections (5% of the total length). In adult scaup, the mean length of each section was 8.4 cm. For ducklings the mean lenghts of each section for the respective age-weight categories were: Ia= 2.3 cm, Ib= 3.8 cm, Ic= 4.8 cm, IIa= 5.8 cm, IIb= 6.3 cm. The diameters of the small intestines were not measured and

therefore, the radial component of spatial segregation was not studied. These standardize length measures provided a correction factor for determining the number of helminths per unit length of intestine but the number of helminths per unit area of intestine could not be calculated.

Each section was opened separately, the mucosal lining was scraped and the contents were washed into a dish of water. Helminths recovered were fixed and preserved in AFA (alcohol-formalin-acetic acid mixture) and identified and counted later, or were identified and counted at necropsy. The presence of some species in the thousands made absolute counts of their populations impractical. In these situations all trematodes, acanthocephalans, and large tapeworms were counted leaving only the small hymenolepidids. The remainder was made up to a standard volume and a one-tenth aliquot was removed and counted.

The results from each duck were tabulated in a species (row) by section (column) matrix. The position of each worm was determined by the location of the scolex; biomass and the extension of the larger tapeworms into succeeding sections were not recorded. A representative example of a data matrix is given in Table 1. A series of such matrices constituted the raw data for further analysis. They are on file in the Department of Zoology, University of Alberta, Edmonton.

Representative cestodes were stained with Blachin's lactic acid carmine (Reichenow et al. 1952) or Ehrlich's hematoxylin, trematodes were stained with Chubb's (1962) acetic acid hematoxylin, and acanthocephalans were cleared in beechwood creosote or lactic acid.

Except for the Hymenolepididae, nomenclature for the helminths follows McDonald (1969). Nomenclature for the hymenolepidids follows Spasskaya (1966) except that the genus *Hymenolepis* (*sensu latu*) was used instead of *Microsomacanthus*.

Table 1. Intraintestinal distribution of helminths recovered from an adult male scaup (*Aythya affinis*) collected June 7, 1974 at Cooking Lake, Alberta

Helminth species	Section of intestine																			Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Fimbriaria fasciolaris	16	20	11																		47
Lateriporus skrjabini				1	1																2
Hymenolepis microskrjabini				22	22	11	11														66
H. tuvensis							11	11	61	94	40										217
Retinometra pittalugai							1														1
H. spinocirrosa							11	30	127	153	100										421
H. abortiva										30	10	333	624	345	250	340	400	170	20		2522
Polymorphus marilis										1	6	11	11	8	5	3					45
H. pusilla																	20	310	300	120	750
																					4071

Analytical Methods

Several of the standard measures of diversity were used to calculate helminth species diversity (HSD). They are:

(1) Number of species = S

(2) Shannon-Weaver (1949) information theory function

$$H' = -\sum_{i=1}^{S} Pi \, Ln \, Pi \quad ,$$

where Pi = proportion of the i-th species (i = 1, 2..., S),

Ln = natural logarithm.

(3) Reciprocal of Simpson's (1949) Index (see Hill 1973)

$$SI = \frac{1}{\sum_{i=1}^{S} (Pi)^2} \quad ,$$

where Pi is as defined above.

(4) Equitability (Pielou 1969)

$$J = \frac{H'}{H'_{max}} \quad ,$$

where H' is as defined above,

H'_{max} = Ln S.

In general, a diversity index should reflect changes in two features of the data, the number of species present and their relative abundances (Peet 1974). Species counts do not consider relative abundance and are strongly influenced by sample size (Krebs 1972). The Shannon function and Simpson's Index incorporate both of these features,

but differ in their sensitivity to the relative abundance component. Hill (1973) has emphasized that these two measures are related to the same basic formula, using different weighting factors for abundance (see Hill for details). As a result, H' is more sensitive to rarer species and SI is more sensitive to the common species. Whittaker (1965) regards SI as a measure of concentration of dominance. Another way of expressing the difference between the two is that H' is a measure of the uncertainty that exists regarding the species of an individual selected at random, whereas SI is a measure of the probability that two individuals selected at random will be the same species.

Measures of niche width and niche overlap, as used by other ecologists, are based on the distribution and overlap of species along particular resource gradients, and are directly applicable to analyzing the distribution and overlap of species along the small intestine.

In this study, I have used Culver's (1972) measure of niche breadth, a standardized Shannon function:

$$B_i = - \sum_{j=1}^{N} p_{ij} \, \mathrm{Ln} \, p_{ij} \div \mathrm{Ln} \, N \quad ,$$

where p_{ij} is the proportion of the i-th species in the j-th section (j = 1, 2..., N).

Percent similarity (used previously for parasite communities by Holmes and Podesta 1968) was used as a measure of habitat niche overlap (HNO) between pairs of species. It is defined as,

$$PS_{ih} = \sum_{j=1}^{N} (\min \, p_{ij}, \, p_{hj}) \quad ,$$

where p_{ij} and p_{hj} are the proportions of species i and h, respectively, in intestinal section j.

This measures the proportion of the individuals of each species which have identical distributions.

Statistical analyses of the data were done on an IBM 360 computer using APL or Fortran. Programs used were obtained from the public libraries of the University of Alberta Computing Center (UACC) or from the Clemson University Statistical Analysis System (SAS) designed by Barr and Goodnight (1972). All tests were based on procedures outlined in Steel and Torrie (1960) or Sokal and Rohlf (1969).

The data were tested for normality of distribution using a program for the Kolmogorov-Smirnov test (UACC: CHER.MYOWN KS). Most of the data were analyzed by analysis of variance (UACC: 2 STP1 ANOVA2, UACC: 2 STP1 ANOVA; SAS: HASP II). T-tests were calculated for unpaired samples (UACC: 160 PSTAT TTEST 4). Product-moment correlation coefficients were determined using UACC: 160 PSTAT CORR and SAS: HASP II.

Other methods of analysis of the data are given when first used.

III. THE HELMINTH FAUNA

The intestinal helminths of anatids are numerous and have been studied extensively (McDonald 1969). In particular, lesser scaup are an important definitive host for many species of intestinal parasites. From 141 adult and 75 duckling scaup collected in central Alberta (primarily from Cooking and Hastings Lakes), Graham (1966) reported 28 species of intestinal helminths, including some species which had individuals numbering in the thousands.

During my study, 82 scaup (30 adults and 52 ducklings) collected from the same two lakes had a total of 33 species of intestinal helminths (26 cestodes, 5 trematodes and 2 acanthocephalans). Data on the prevalence and intensity of each species are summarized in Table 2. Cestodes were the most important group, accounting for 98 percent of the total number of helminths. In particular, high numbers of small tapeworms of the genus *Hymenolepis* were major components of the fauna.

Individual species of helminths were ranked according to their relative abundances (prevalence × mean intensity) (Table 3). The most abundant species, plus three others (*Fimbriaria fasciolaris*, *Lateriporus skrjabini*, *Dicranotaenia coronula*), generally present in lower numbers but considerably larger than the other species, were considered to be the dominant species. These species, indicated by asterisks in Table 3, will be given special attention in the remainder of this thesis.

For comparative purposes the abundance values for the species of intestinal helminths reported by Graham (1966) and those from 18 scaup ducklings collected from potholes in southern Alberta during the mid-1960's (unpublished records) were determined (Table 3). With few

Table 2. Intestinal helminths recovered from lesser scaup (*Aythya affinis*) from Cooking and Hastings Lakes, Alberta, 1973-74

Age	Adults		Ducklings	
Number examined	30		52	
Helminths	Prevalence %	Intensity Mean (Range)	Prevalence %	Intensity Mean (Range)
Cestoda				
Hymenolepididae				
Anatinella spinulosa	13	19 (1-61)	2	1 (1)
Dicranotaenia coronula	47	27 (1-79)	52	6 (1-24)
Diorchis excentricus	47	32 (1-246)	10	17 (5-36)
D. inflata	3	1 (1)		
D. nyrocoides	3	1 (1)	4	91 (18-164)
D. ransomi	3	8 (8)	4	10 (8-12)
D. spinata	3	101 (101)		
Diorchis n. sp. (hooks 44 μ)	30	106 (1-428)	10	3 (1-7)
Diorchis sp. (hooks 28 μ)	3	83 (83)		
Fimbriaria fasciolaris	100	193 (5-1166)	87	83 (1-205)
Hymenolepis abortiva	97	5432 (8-21035)	65	206 (6-969)
H. albertensis	7	35 (30-40)	67	164 (1-480)
H. arcuata	10	3 (1-5)		
H. compressa	3	34 (34)		
H. fausti	20	77 (12-225)	19	441 (1-1485)
H. microskrjabini	57	1808 (11-29785)	85	302 (3-2292)
H. pusilla	90	3044 (85-15700)	81	166 (2-550)
H. recurvata	40	320 (2-1850)	2	10 (10)
H. spinocirrosa	97	7608 (394-28751)	96	1025 (1-6321)
H. spiralibursata	7	15 (10-20)	27	19 (3-41)
H. tuvensis	83	1218 (5-10982)	75	221 (1-1014)
Hymenolepis sp. (hooks 40 μ)	3	23 (23)		

Table 2 (continued)

Age Number examined	Adults 30		Ducklings 52	
Helminths	Prevalence %	Intensity Mean (Range)	Prevalence %	Intensity Mean (Range)
Retinometra pittalugai	83	667 (1-7282)	23	14 (1-77)
Sobolevicanthus gracilis	23	67 (1-424)	8	8 (1-28)
Sobolevicanthus n. sp. (hooks 69 µ)			2	8 (8)
Dilepididae				
Lateriporus skrjabini	60	38 (2-177)	48	12 (1-93)
Trematoda				
Strigeidae				
Apatemon gracilis	57	23 (1-132)	6	4 (1-6)
Cotylurus hebraicus	20	33 (2-108)		
Echinostomatidae				
Echinoparyphium recurvatum	20	151 (2-881)	15	7 (1-33)
Notocotylidae				
Notocotylus attenuatus			14	3
Plagiorchidae				
Plagiorchis sp.			4	2 (1-3)
Acanthocephala				
Polymorphidae				
Corynosoma constrictum	3	3 (3)	19	4 (1-10)
Polymorphus marilis	100	60 (6-277)	65	7 (1-39)

Table 3. Abundance of the intestinal parasites of lesser scaup in three surveys in Alberta

Helminth species	Adults				Ducklings					
	Present study		Graham (1966)		Present study		Graham (1966)		Unpublished records[c]	
Hymenolepis spinocirrosa	[a]7380	(1)[b]*	115	(1)	984	(1)*	65	(2)	3098	(1)
H. abortiva	5269	(2)*	51	(3)	134	(5)*	30	(3)	660	(5)
H. pusilla	2740	(3)*	-		135	(4)*	-		2450	(3)
H. microskrjabini	1031	(4)*	-		257	(2)*	-		-	
H. tuvensis	1011	(5)*	83	(2)	166	(3)*	111	(1)	3038	(2)
Retinometra pittalugai	554	(6)*	5	(7)	3.2	(13)	.5	(12)	48	(15)
Fimbriaria fasciolaris	193	(7)*	4	(8)	72	(8)*	11	(4)	170	(8)
H. recurvata	128	(8)*	-		.2	(23)	-		.5	(26)
Polymorphus marilis	60	(9)*	20	(4)	4.6	(11)*	4.2	(8)	8	(18)
Diorchis n. sp. (hooks 44 μ)	32	(10)	-		.3	(21)	-		-	
Echinoparyphium recurvatum	30	(11)	.8	(12)	1.1	(16)	.5	(13)	1	(24)
Lateriporus skrjabini	23	(12)*	6	(6)	5.8	(9)*	5	(7)	49	(14)
Sobolevicanthus gracilis	15	(13)	-		.6	(18)	-		2	(21)
H. fausti	15	(14)	-		84	(7)*	-		102	(9)
Diorchis excentricus	15	(15)	-		1.7	(15)	-		.5	(25)
Apatemon gracilis	13	(16)	2	(11)	.2	(22)	1.8	(9)	27	(16)
Dicranotaenia coronula	13	(17)*	3	(9)	3.1	(14)*	.5	(15)	1.5	(22)
Cotylurus hebraicus	7	(18)	.6	(13)	-		.5	(14)	50	(13)
Diorchus spinata	3	(19)	.2	(17)	-		.04	(19)	66	(11)
Diorchis sp. (hooks 28 μ)	2.5	(20)	-		-		-		-	
Anatinella spinulosa	2.5	(21)	-		.02	(26)	-		-	
H. albertensis	2.5	(22)	-		110	(6)*	-		-	
H. spiralibursata	1.1	(23)	3	(10)	5.1	(10)	1.1	(10)	11	(17)
H. compressa	1	(24)	-		-		9.2	(5)	385	(6)
Hymenolepis sp. (hooks 40 μ)	.7	(25)	-		-		-		-	
H. arcuata	.3	(26)	.1	(19)	-		.03	(20)	-	
Diorchis ransomi	.2	(27)	-		.4	(20)	-		.3	(27)

Table 3 (continued)

Helminth species	Adults		Ducklings		
	Present study	Graham (1966)	Present study	Graham (1966)	Unpublished records[c]
Corynosoma constrictum	.09(28)	.2 (16)	.8 (17)	-	1.5 (23)
Diorchis inflata	.03(29)	-	-	-	65 (12)
Diorchis nyrocoides	.03(30)	-	3.6 (12)	-	-
Notocotylus attenuatus	-	.01(26)	.4 (19)	-	-
Sobolevicanthus sp. (hooks 69 μ)	-	.5 (14)	.2 (24)	.3 (16)	-
Plagiorchis sp.	-	-	.08(25)	-	-
H. parvula	-	10 (5)	-	.7 (11)	825 (4)
R. cyrtoides	-	.5 (15)	-	.07(18)	93 (10)
Oligorchis sp.	-	.1 (18)	-	.08(17)	-
L. mathevossianae	-	.06(20)	-	.01(21)	-
Anomotaenia ciliata	-	.03(21)	-	-	.3 (28)
Echinostoma revolutum	-	.01(23)	-	-	.2 (29)
Schistocephalus solidus	-	.01(24)	-	-	-
Psilochasmus oxyurus	-	.01(25)	-	-	-
S. octacantha	-	-	-	6.9 (6)	.2 (30)
H. tenuirostris	-	-	-	-	6 (20)
H. trombidicantha	-	-	-	-	268 (7)
Streptocara crassicauda	-	-	-	-	6.6 (19)

a = abundance value = prevalence x mean intensity.

b = rank.

c = based on 18 scaup ducklings collected from potholes in southern Alberta; identified by R. Podesta.

* = signifies dominant species from the present study, see text p.10 for basis of selection.

exceptions, the same species dominated all three sets of data. Notable differences were the absences of *H. pusilla*, *H. recurvata* and *H. fausti* from Graham's data, *H. microskrjabini* and *H. albertensis* from both of the other studies, and *H. compressa* and *H. parvula* from my data. Of these species, *H. albertensis* is a parasite of white-winged scoters, which were more abundant in the Cooking-Hastings lake system during my study than during Graham's (Holmes, pers. comm.), and were not present in the potholes in southern Alberta. *Hymenolepis compressa* is a species characteristic of sloughs and potholes; the specimens in Graham's study actually came from sloughs near Cooking Lake, not the lake itself. The other species are regarded by McDonald (1969) as uncommon parasites in waterfowl, and at this time no explanation can be given for their sporadic occurrence.

In general, abundance values were substantially lower in Graham's data than in the other two studies. Abundance values in the southern Alberta ducklings were similar to those in my adults. The lower abundance values in Graham's study may be due to a reduction in water levels in Cooking and Hastings Lakes since the mid-1960's. As a result, there has been a change in the species of waterfowl that use these lakes during the nesting season, and probably, therefore, in parasite faunas. Populations of ruddy ducks (*Oxyura jamaicensis*) have virtually vanished, those of red-necked grebes and coots (*Fulica americana*) have decreased, while those of white-winged scoters and of several species of dabbling ducks have increased markedly. Scaup have remained about the same (Holmes, pers. comm.).

It is important to note that most of the dominant species of parasites are found almost exclusively in scaup in the study area.

They are only rarely encountered in other waterfowl (Graham 1966; unpublished records). In Appendix I, scaup are listed as the main host (defined by Sulgostowska [1958] as that host [or hosts] in which the mature parasite reaches maximal abundance) for these species.

There are only three exceptions to this general rule. *Fimbriaria fasciolaris* and *D. coronula* are common in a wide variety of diving and dabbling ducks (McDonald 1969; unpublished records); in the study area, no main host can be singled out. As indicated earlier, *H. albertensis* (an important helminth of ducklings in the present study) is primarily a parasite of white-winged scoters (unpublished records); scaup (ducklings) appear to be an auxillary host (defined by Sulgostowska [1958] as a host in which mature parasites are less abundant than in the main host) (Appendix I).

All of the helminths reported in Table 2 have indirect life cycles requiring aquatic invertebrates as intermediate hosts. Scaup are omnivorous; every study on their diets has noted the importance of invertebrates, and particularly amphipods, which usually constitute over half of their food (Sugden 1973). Given that scaup are the main hosts for almost all their dominant helminths, and that amphipods make up such an important part of their diet, it is not surprising that amphipods (*Gammarus lacustris* and *Hyalella azteca*) are the major intermediate hosts for most of the dominant species of helminths in the Cooking-Hastings Lakes study area (Denny 1969; Podesta and Holmes 1970) (Appendix I). The life cycles of *D. coronula*, *H. fausti*, and *Retinometra pittalugai* have not been determined in the study lakes, but studies elsewhere indicate a wide variety of invertebrates, including cladocerans,

copepods, ostracods and snails, can serve as intermediate hosts (Czaplinski 1956; Jarecka 1958, 1961; Spasskaya 1966; McDonald 1969; Valkounova 1973). The life cycle of *H. recurvata* is unknown (McDonald 1969).

The minimum generation times of many of the dominant cestodes of scaup are very short. Infective cysticercoids of several species may develop in as little as 8 or 9 days at approximately 20°C (Denny 1969; Podesta and Holmes 1970). Under experimental conditions, egg packets have appeared in the feces of infected scaup in as little as 4 to 6 days. Therefore, minimum generation times may be less than 2 weeks. Where known, developmental times are given in Appendix I.

IV. TEMPORAL ASPECTS OF COMMUNITY STRUCTURE

There were minor fluctuations in the total helminth community of adult scaup (Table 4), but during the period of time the scaup were restricted to the nesting grounds there were no significant differences (by season or year) in the number of helminths (total, mean, mean number per centimeter of intestine) or in any of the measures of faunal diversity.

Mean numbers of the dominant species also fluctuated (Fig. 1; Appendix II), but statistically significant seasonal differences were found in only four species. Populations of *F. fasciolaris* and *P. marilis* increased significantly with season (see Appendix II for F values and levels of significance). Populations of *H. spinocirrosa* were high initially, declined in mid-summer, followed by an increase in numbers by early August. *Hymenolepis recurvata* was absent in the late summer samples; it was the only dominant helminth that showed such a seasonal limitation.

The youngest scaup ducklings examined (class Ia, collected in 1974) were only approximately 3 days old, weighed only 30 to 35 grams, and still retained functional yolk sacs. All six of these birds were infected with *H. spinocirrosa*; five other species, including *F. fasciolaris* and *H. pusilla*, were found in one or two birds each. There was a mean of two species and 15 individuals per bird (Table 5). All of the tapeworms were just beginning to strobilate.

The youngest ducklings examined in 1973 were approximately 4 to 5 days old, weighed 35 to 42 grams (mean, 39g), and had completely absorbed the yolk. Their parasite communities were much better developed,

Table 4. Seasonal variation in population sizes and helminth species diversity from adult lesser scaup (± standard deviation)

	1973			1974		
No. examined:	June 5	July 5	August 5	June 5	July 5	August 5
Mean number of helminths/ bird	29869±20634	19033±8082	23710±14030	8928±4774	7408±10138	24706±20188
Number of helminths/cm of gut	176.7±122.1	112.6±47.8	140.2±83.1	53.5±29.7	38.2±49.8	114.1±80.8
Number of species (S)	21	18	18	16	23	21
Mean number of species/ bird	12.6±2.5	11.2±1.5	9.8±1.8	11.2±1.9	13.2±3.1	11±3.1
Shannon diversity (H)	1.14±.18	1.23±.18	1.31±.22	1.22±.23	1.65±.40	1.22±.23
Simpson's Index (SI)	2.54±.50	2.63±.38	3.02±.63	2.70±.85	4.20±1.43	2.80±.75
Equitability (J)	.45±.06	.51±.07	.58±.07	.50±.07	.65±.16	.51±.10

Figure 1. Seasonal dynamics of the dominant species of helminths from 30 adult lesser scaup collected at Cooking and Hastings Lakes, Alberta, June-August, 1973-74.

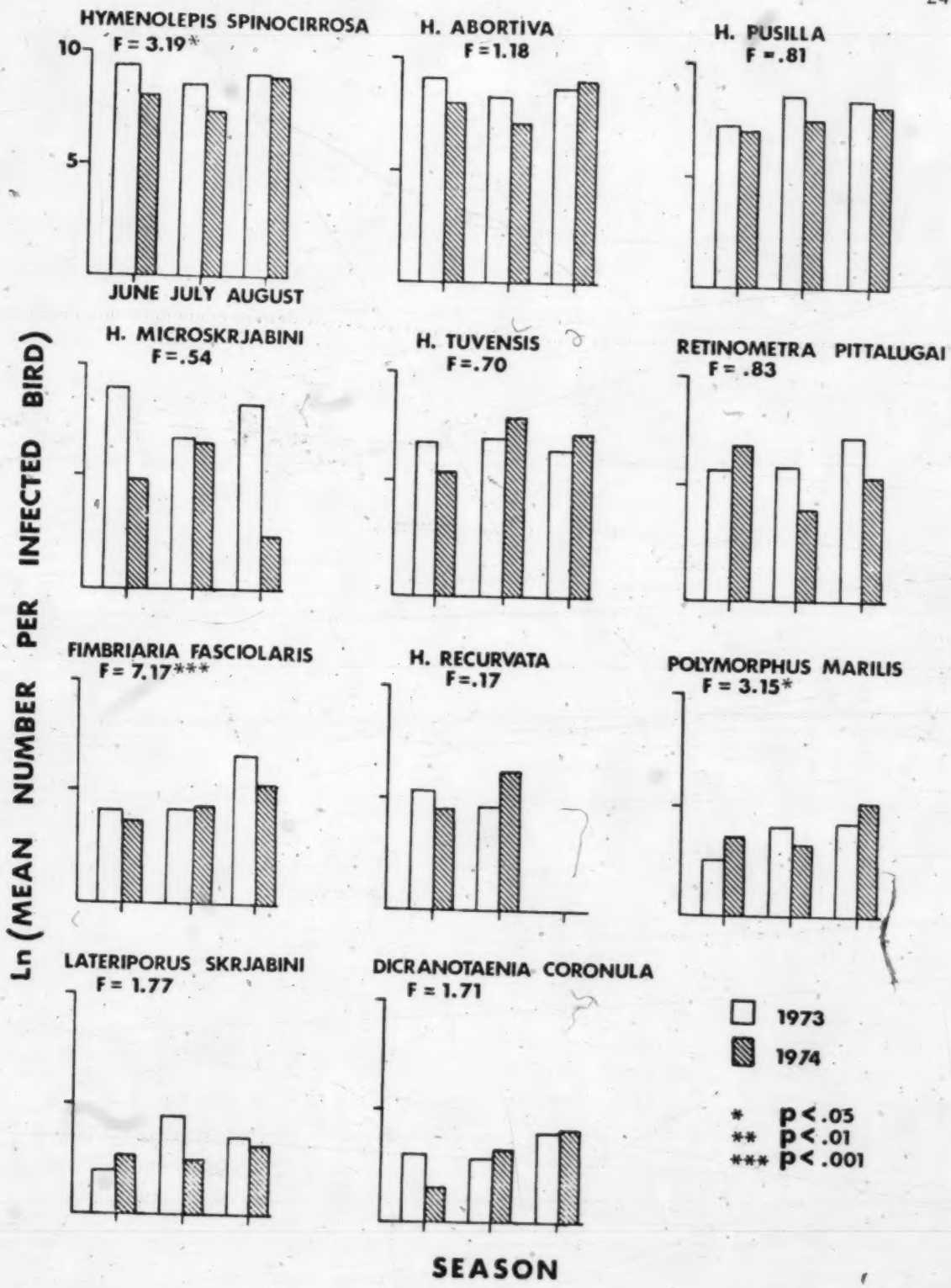

HYMENOLEPIS SPINOCIRROSA
F = 3.19*
H. ABORTIVA
F = 1.18
H. PUSILLA
F = .81
10
5
JUNE JULY AUGUST
H. MICROSKRJABINI
F = .54
H. TUVENSIS
F = .70
RETINOMETRA PITTALUGAI
F = .83
FIMBRIARIA FASCIOLARIS
F = 7.17***
H. RECURVATA
F = .17
POLYMORPHUS MARILIS
F = 3.15*
LATERIPORUS SKRJABINI
F = 1.77
DICRANOTAENIA CORONULA
F = 1.71
1973
1974
* p < .05
** p < .01
*** p < .001
Ln (MEAN NUMBER PER INFECTED BIRD)
SEASON

Table 5. Acquisition of helminths by five age-weight categories of lesser scaup ducklings collected at Cooking and Hastings Lakes, Alberta, 1973-74

Age category:	I_a	I_b	I_c	II_a	II_b	ANOUA Results (I_a - II_b) F	Adults (collected same period of time: late July)
No. examined: 1973[a]	5	5	6	5	6		
1974[b]	6	6	5	3	2[c]		
Mean number of helminths/bird	[a]965±624 [b]15±17	1374±631 1763±1467	1671±925 1699±952	3537±1114 2375±683	4529±2363 2406±1223	6.74****	[a]23710±14030 [b]24706±20188
Number of helminths/cm of gut	[a]11.2±7.3 [b].4±.4	13.3±6.1 24.0±19.6	13.3±7.3 17.5±9.1	26.0±8.2 20.8±8.1	30.6±16.0 19.9±11.0	4.09*+	[a]140.2±83.1 [b]114.2±80.8
Number of species (S)	[a]14 [b]6	14 17	16 14	17 17	18 12	19.86****+	[a]18 [b]21
Mean number of species/bird	[a]9.2±2.2 [b]2.0±.7	9.4±1.1 9.3±.6	10.1±.8 8.8±2.2	11.4±.6 13.0±3.0	12.3±2.1 10.5±.7	3.15*	[a]9.8±1.8 [b]11.0±3.1
Shannon diversity (H)	[a]1.3±.34 [b].43±.30	1.24±.30 .62±.34	1.66±.18 1.15±.37	1.33±.24 1.49±.47	1.51±.29 1.57±.11	8.72***	[a]1.31±.22 [b]1.22±.23
Simpson's Index (SI)	[a]2.88±1.04 [b]1.46±.39	2.56±1.08 1.48±.45	4.20±1.19 2.52±1.15	2.72±.86 3.54±2.2	3.64±1.42 3.39±.34	3.28*	[a]3.02±.63 [b]2.80±.75
Equitability (J)	[a].60±.12 [b].56±.37	.55±.11 .29±.17	.72±.07 .53±.15	.55±.11 .58±.17	.60±.09 .67±.02	3.41*	[a].58±.07 [b].51±.10
Mean weights (g)	[a]39±3 [b]32±2	68±16 54±11	112±20 102±10	194±30 182±42	305±37 286±16	-	[a]612±40 [b]582±109
Age (days)	0-5	6-10	11-15	16-20	21-30	-	

c = does not include 3 birds with exceptionally high populations of *Hymenolepis fausti*

*p < .05; **p < .01; ***p < .001.

+ indicates significant linear regression.

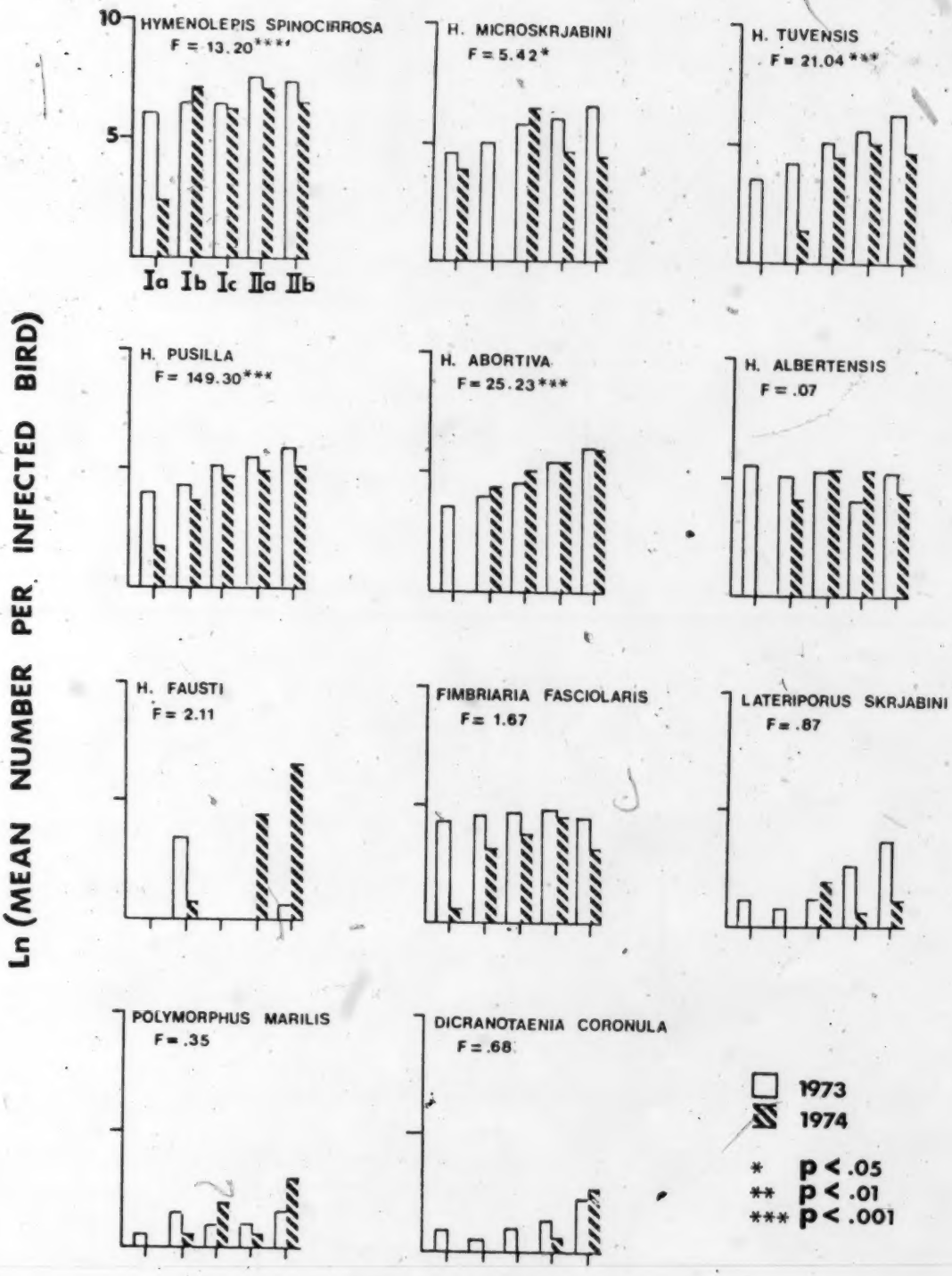
with a mean of 965 individuals (342-1899) belonging to a mean of nine species (7-12). Almost all of these birds contained reasonably high populations of most of the dominant species, including *H. spinocirrosa*, *H. microskrjabini*, *H. tuvensis*, *H. pusilla*, *H. albertensis*, and *F. fasciolaris*. Mature specimens (those having proglottids containing fully developed reproductive organs) of all except *H. pusilla* were present (Appendix III), and at least some of the *H. spinocirrosa* and *H. albertensis* were already gravid.

By the time the birds were 6 to 10 days old (class Ib), they had a mean of 1586 individuals (296-4445) belonging to a mean of nine species (7-12), with no significant difference between years (Table 5). All the dominant helminths were present (Appendix III).

With further increases in host age, the community continued to develop. There were significant positive linear regressions on age for the total number of helminths ($r = .77$, $p < .025$), the mean number per centimeter of intestine ($r = .86$, $p < .001$), and the total number of species ($r = .81$, $p < .001$). Measures of faunal diversity differed significantly between age categories, but showed no consistent pattern (Table 5).

As expected, populations of most of the dominant helminths increased with age of the host (Fig. 2, Appendix III). However, sample sizes were small, and the increase was statistically significant only for *H. abortiva*, *H. microskrjabini*, *H. pusilla*, *H. spinocirrosa*, and *H. tuvensis* in 1973 and *F. fasciolaris* in 1974. Within the ages of ducklings sampled, there was no evidence that any of the parasites were specialists using the younger ducklings.

Figure 2. Acquisition of the dominant helminths from 52 lesser scaup ducklings collected at Cooking and Hastings Lakes, Alberta, late July, 1973-74.


HYMENOLEPIS SPINOCIRROSA
F = 13.20****
H. MICROSKRJABINI
F = 5.42*
H. TUVENSIS
F = 21.04***
H. PUSILLA
F = 149.30***
H. ABORTIVA
F = 25.23***
H. ALBERTENSIS
F = .07
H. FAUSTI
F = 2.11
FIMBRIARIA FASCIOLARIS
F = 1.67
LATERIPORUS SKRJABINI
F = .87
POLYMORPHUS MARILIS
F = .35
DICRANOTAENIA CORONULA
F = .68
10
5
Ia Ib Ic IIa IIb
1973
1974
* p < .05
** p < .01
*** p < .001
Ln (MEAN NUMBER PER INFECTED BIRD)
AGE

However, when the communities of helminths in ducklings are compared with those in adult scaup, two species appear to be temporally limited. *Hymenolepis albertensis* was abundant in young scaup, but rare and never mature in adults. *Retinometra pittalugai* was abundant in adults, but rare in ducklings (except for the largest ducklings collected in 1973).

Discussion

Graham (1966) has also studied the effects of season and age on the parasites of scaup from Cooking and Hastings Lakes. He reported the seasonal patterns of abundance of six of the dominant species from this study. In both studies *F. fasciolaris*, *L. skrjabini* and *P. marilis* increased in abundance from June through August. In Graham's study *D. coronula* increased from June to July then disappeared by August, whereas in my study, it increased in abundance over the summer. *Hymenolepis tuvensis* also showed different patterns between the two studies; in Graham's study it had minimal populations in mid-summer, whereas in my study there were maximum populations in mid-summer. The patterns of *R. pittalugai* were variable between the two studies and between the two years of my study.

These comparisons suggest *F. fasciolaris*, *L. skrjabini* and *P. marilis* probably have consistent seasonal patterns dependant upon their general biology. All three are relatively large, long-lived worms, especially when compared with the small hymenolepidids. Existing in a complex community with these features would seem to require a good competitive ability. If so, their increases in abundance during the

summer is not surprising. *Dicranotaenia coronula* also shows these same features, so the same arguments should apply. In my data it did increase in abundance over the summer. Populations of smaller hymenolepidids appear to be more labile, responding more quickly to local conditions. This appears to be the situation with *R. pittalugai*.

Previous studies indicate that young waterbirds acquire helminths rapidly and may harbor species that are not found in adults (Wehr and Herman 1954; Cornwell and Cowan 1963; Buscher 1965; Colbo 1965; Neraasen 1970). In Graham's (1966) study of scaup, a few ducklings had acquired helminths by the time they were about 3 days old (30g). It was not until they had reached approximately 3 weeks of age (100-200g) that all were infected. During the first three weeks relatively few individual parasites were acquired (median number less than 20). Ducklings over 200g had approximately the same number of parasites as adults (median numbers approximately 75), and those over 400g had more parasites than adults.

In comparison, all of the ducklings that I examined, even those approximately 3 days old, were infected. In addition they acquired individual parasites much more rapidly; by the time they were 5 days old they harbored a mean of 965 worms and by the time they were 2 weeks old a mean of over 1600 worms. It should be noted that adults were also much more heavily parasitized in my study (overall mean 18,900).

Neraasen (1970) suggested that an important factor in the production of high populations of helminths in goslings was the short generation time of many of the species of parasites. In my study, gravid specimens of several species (*H. abortiva*, *H. albertensis*, *H. microskrjabini*,

H. spinocirrosa, *H. tuvensis*) were recovered from ducklings less than 1 week old. Under experimental conditions the generation times of these species (except for *H. abortiva* which has not been determined) are approximately 14 days (see Appendix I for details). These relatively short generation times, when combined with high populations of definitive and intermediate hosts, result in the dispersal of large numbers of infective stages. This is clearly an important feature in the rapid development and dynamic nature of the helminth community of scaup, particularly in ducklings.

One of those species that developed particularly rapidly in ducklings was *H. albertensis*, in which maximum populations were found in ducklings 15 to 20 days old. The high numbers of gravid individuals in the young ducklings and the virtual absence of this species in adult scaup are clear evidence of temporal limitation on the basis of age of the host. However, Denny (1969) recovered mature specimens of *H. albertensis* from an experimentally infected laboratory-reared scaup 8 days post-infection, indicating that in the absence of other species of parasites, adult scaup are satisfactory hosts. When combined with my data, these observations support the hypothesis that *H. albertensis* is an opportunistic species (as defined by MacArthur, 1960) with the ability to invade, colonize and reproduce rapidly before being displaced by competitively superior species. It appears to be replaced by *R. pittalugai* in adults, which is rare in ducklings. These two species then appear to be temporally segregated, ecological equivalents.

In conclusion, the data suggest that neither seasonal aspects (at least during the time the birds are restricted to the nesting grounds)

nor host age aspects of temporal segregation are particularly important in determining the complexity of the intestinal helminth community of lesser scaup. Only one species was limited seasonally in adults (*H. recurvata*) and it was not replaced by a new species. There was evidence of temporal segregation of two species (*H. albertensis* in ducklings, *R. pittalugai* in adults) on the basis of host age. Overall, the community is comprised of a well established fauna and the regulation of their populations must be explained on bases other than those related to temporal segregation.

V. SPATIAL ASPECTS OF COMMUNITY STRUCTURE

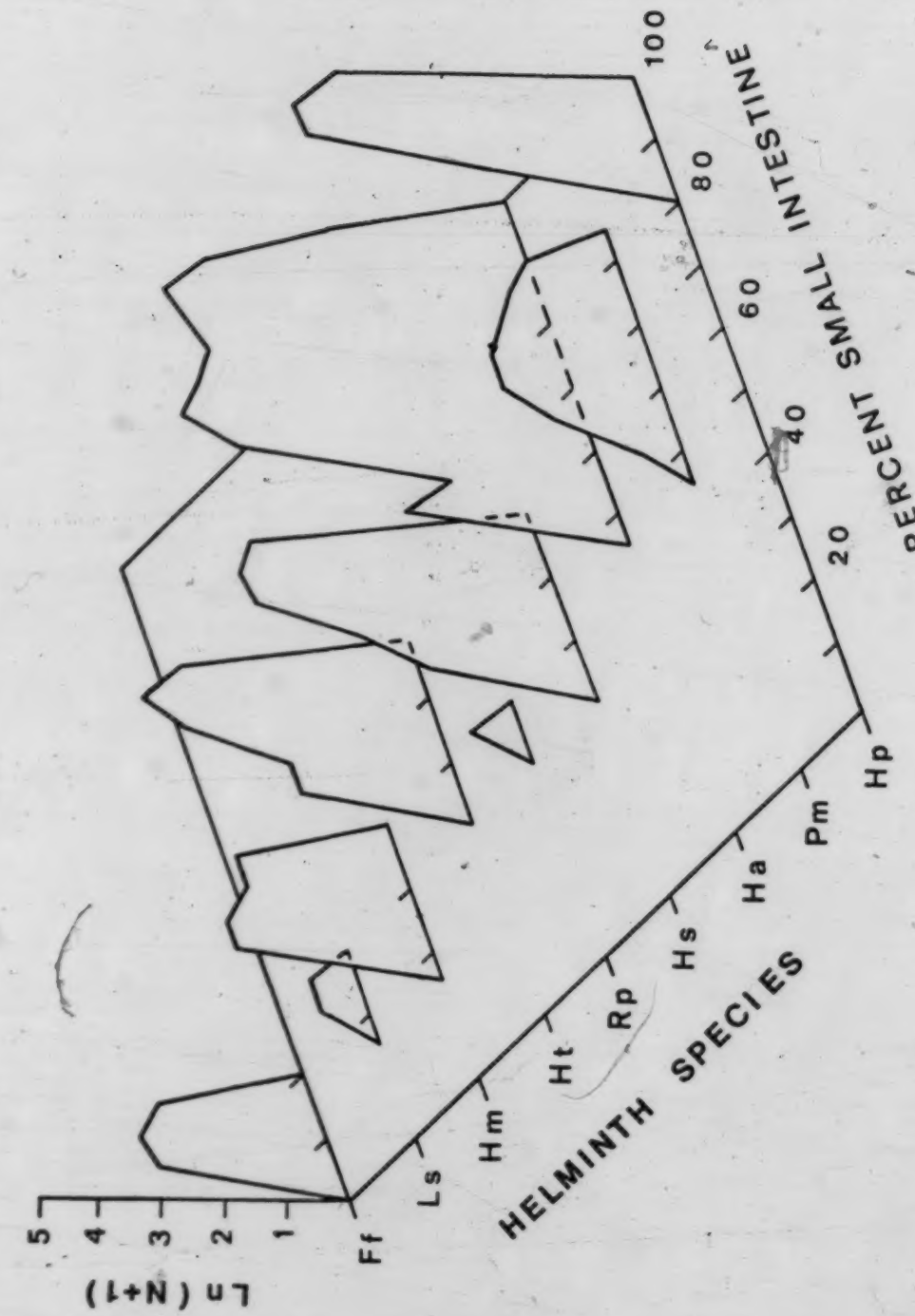
Each of the helminths of scaup was limited in its distribution along the small intestine, and the distribution of each overlapped that of one or more other species. As an example, the intraintestinal distributions of all species found in a representative individual scaup are shown in Figure 3. Data from each individual bird were used to calculate the helminth species diversity of each 5 percent section of the intestine, the intraintestinal distribution of each species and the habitat niche overlaps between all pairs of species in that bird. Variability in the communities in different birds could then be assessed by treating these derived data statistically. The following sections investigate the importance of these spatial components in the development and structure of the intestinal helminth community of scaup.

Intraintestinal Helminth Species Diversity

In my study I have used the helminths from the small intestines of individual scaup to study patterns of helminth species diversity (HSD) along what may be considered to be a complex resource gradient. The basic data set consisted of four measures of HSD (S = number of species; H' = Shannon diversity; J = equitability; SI = Simpson's Index) calculated for each of the 20 equal sections of the small intestine of each of the 82 individual birds.

Data on each measure of HSD in adult scaup were tested, using an analysis of variance, for differences associated with year and season. Each section was examined separately. No significant differences were found; therefore, data from all of the adult scaup were combined to give

Figure 3. Intraintestinal distribution of helminths recovered from an adult male scaup (*Aythya affinis*) collected June 7, 1974 at Cooking Lake, Alberta (see Table 1 for data; Ff = *Fimbriaria fasciolaris*, Ls = *Lateriporus skrjabini*, Hm = *Hymenolepis microskrjabini*, Ht = *H. tuvensis*, Rp = *Retinometra pittalugai*, Hs = *H. spinocirrosa*, Ha = *H. abortiva*, Pm = *Polymorphus marilis*, Hp = *H. pusilla*)


L_n (N+1)
5
4
3
2
1
Ff
Ls
Hm
Ht
Rp
Hs
Ha
Pm
Hp
HELMINTH SPECIES
20
40
60
80
100
PERCENT SMALL INTESTINE

a single value for each section (Table 6). A one-way analysis of variance of these data indicated that for each measure there was a significant variance associated with location (section number) and that most of this variance could be explained by a regression of HSD on location. For J only the linear component explained a significant component of the variance, for H' and SI a quadratic regression accounted for the majority of the variance and for S the quadratic regression accounted for most of the variance, but a significant portion was accounted for by a cubic component (Table 7). The regressions for each of these measures of HSD in adult scaup are shown by solid lines in Figure 4.

The patterns shown by H, J and SI are fairly consistent, with diversity declining throughout, but with relatively little loss of diversity through the anterior two-thirds to three-fourths of the intestine, followed by a relatively rapid loss of diversity in the posterior ileum (at least in H and SI). The number of species (S), however, demonstrated a different pattern, with maximal values in the third quarter of the intestine. This different pattern was apparently due to the presence of high numbers of relatively rare species in this part of the intestine. The populations of these species were low, and consequently they had relatively little influence on the other measures of HSD.

Similarly, data from ducklings were tested for differences associated with year and age class, testing each section separately. Again, no significant differences were found. Therefore, data from all ducklings were combined to give a single value for each section (Table 8).

Table 6. Means ± standard deviations of helminth species diversity along the small intestines of 30 adult lesser scaup collected during the summers of 1973-74 from Cooking and Hastings Lakes, Alberta

Section of intestine	S*	H	J	SI
1	2.0±1.2	.39±.41	.39±.41	1.41±.67
2	2.7±1.3	.56±.40	.56±.34	1.70±.74
3	2.7±1.3	.55±.35	.54±.36	1.61±.70
4	2.8±1.0	.53±.32	.56±.29	1.62±.47
5	2.5±1.2	.42±.32	.46±.34	1.43±.52
6	2.8±1.5	.46±.38	.41±.31	1.50±.59
7	3.0±1.3	.50±.42	.43±.33	1.61±.69
8	2.7±1.0	.38±.33	.35±.29	1.40±.44
9	2.5±1.0	.37±.28	.37±.27	1.41±.42
10	3.0±1.4	.40±.34	.30±.23	1.41±.50
11	3.2±1.1	.46±.30	.41±.27	1.52±.45
12	3.3±1.2	.44±.37	.36±.24	1.51±.59
13	2.9±1.2	.38±.40	.31±.28	1.40±.63
14	3.1±1.2	.36±.35	.29±.27	1.40±.49
15	3.0±1.1	.39±.33	.35±.27	1.31±.53
16	2.7±1.2	.36±.34	.34±.29	1.40±.50
17	2.7±0.8	.27±.25	.27±.24	1.21±.25
18	2.4±1.2	.29±.31	.31±.34	1.32±.39
19	1.8±0.7	.12±.20	.15±.24	1.11±.21
20	1.3±0.7	.09±.22	.11±.26	1.00±.40

*S = Number of species.

H = Shannon formula.

J = Equitability.

SI = Simpson's Index.

Table 7. Analysis of variance of measures of helminth species diversity between equal five-percent sections of the small intestine of 30 adult lesser scaup (% = percent of variance accounted for by regression)

Source	Species			Shannon diversity			Equitability			Simpson's Index		
	SS	F	%	SS	F	%	SS	F	%	SS	F	%
Regression	3.695	22.510***	.809	.234	23.081***	.821	.197	16.455***	.755	.399	15.491***	.744
Linear	.265	4.837*	.058	.191	56.634***	.670	.191	47.842***	.732	.352	40.970***	.657
Quadratic	2.889	52.796***	.632	.035	10.290**	.123	.004		.015	.038	4.464*	.071
Cubic	.541	9.893**	.118	.008		.028	.002		.008	.009		.017
Error	.875			.054			.064		.245	.137		.256

* = $p<.05$

** = $p<.01$

*** = $p<.001$

Figure 4. Pattern of intraintestinal helminth species diversity along the small intestine of adult (solid line) and duckling (dashed line) lesser scaup (S = number of species; H' = Shannon diversity; J = equitability; SI = Simpson's Index).

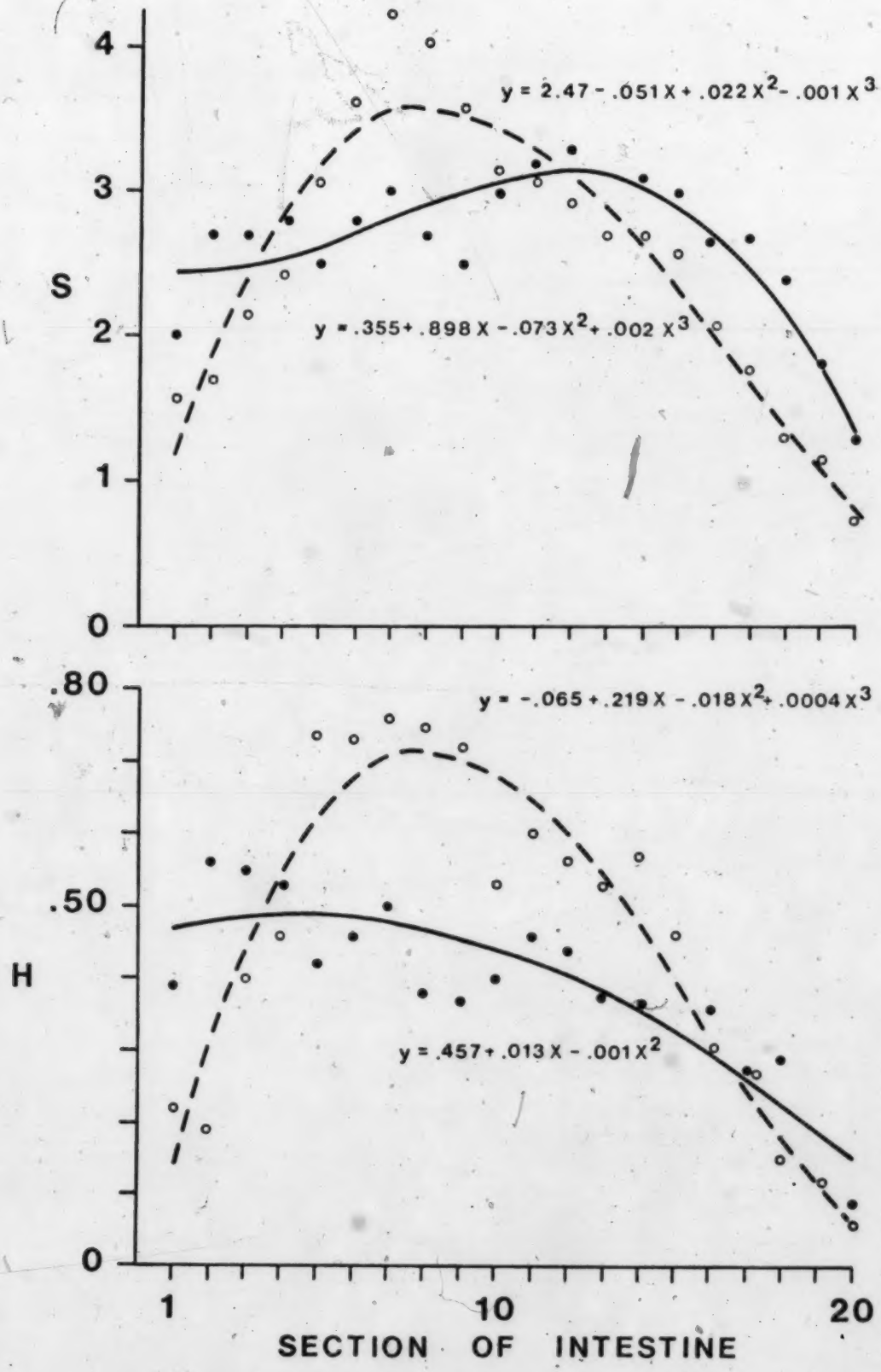

y = 2.47 - .051X + .022X² - .001X³
y = .355 + .898X - .073X² + .002X³
S
4
3
2
1
0
y = -.065 + .219X - .018X² + .0004X³
y = .457 + .013X - .001X²
H
.80
.50
0
1
10
20
SECTION OF INTESTINE

Figure 4 (contd.)

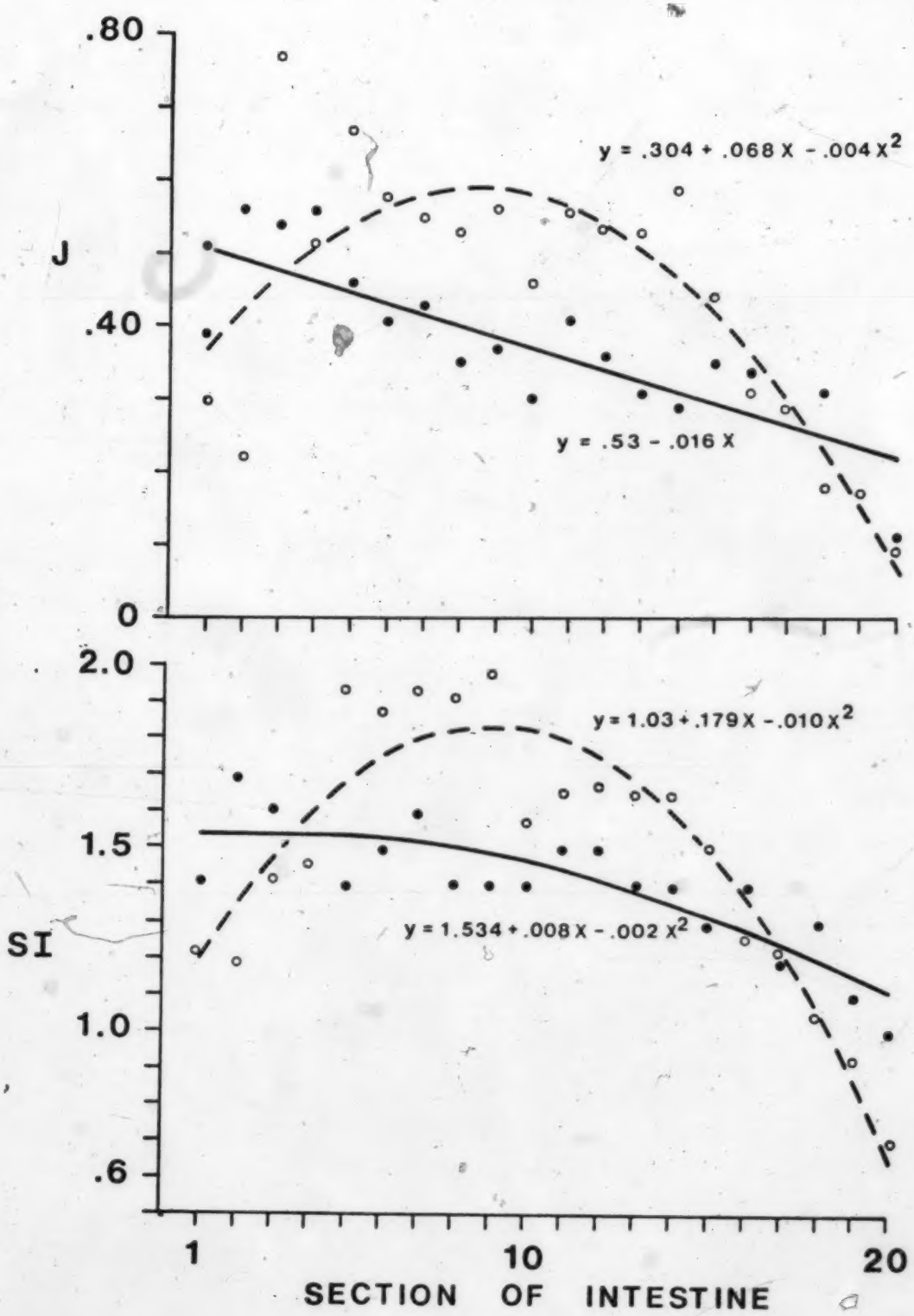


Table 8. Means ± standard deviations of helminth species diversity along the small intestines of 43 lesser scaup ducklings collected during late July, 1973-74 from Cooking and Hastings Lakes, Alberta (abbreviations as in Table 6)

Section of intestine	S	H	J	SI
1	1.6± .6	.22±.26	.30± .36	1.21±.29
2	1.7± .9	.19±.28	.22± .29	1.19±.37
3	2.2± .9	.40±.34	.77±1.86	1.42±.49
4	2.4± .9	.46±.26	.51± .29	1.46±.35
5	3.1±1.0	.74±.32	.67± .27	1.94±.60
6	3.6±1.0	.73±.33	.58± .24	1.88±.66
7	4.3±1.5	.76±.35	.55± .19	1.94±.81
8	4.1±1.1	.75±.37	.53± .22	1.92±.73
9	3.6±1.3	.72±.43	.56± .28	1.99±.85
10	3.2±1.4	.53±.35	.46± .30	1.58±.53
11	3.1±1.1	.60±.28	.56± .27	1.66±.47
12	2.9±1.5	.56±.38	.54± .31	1.68±.67
13	2.7±1.0	.53±.39	.53± .33	1.66±.73
14	2.7±1.1	.57±.31	.59± .31	1.65±.54
15	2.6±1.3	.46±.37	.44± .35	1.51±.53
16	2.0±1.1	.29±.34	.31± .32	1.27±.52
17	1.8±1.1	.27±.37	.29± .37	1.23±.63
18	1.3± .7	.15±.26	.18± .31	1.05±.50
19	1.2± .8	.12±.22	.17± .31	.93±.52
20	.7± .7	.06±.18	.09± .26	.70±.58

An analysis of variance for these data indicated that for each measure there was a significant variation associated with location. There were significant curvilinear regressions on location (section number) for all of the measures (Table 9). In each case, diversity was low at each end of the intestine and high throughout the mid-region; the patterns of J and SI were best fitted by quadratic regressions, those of S and H' were best fitted by cubic regressions. The pattern for each of these measures of HSD in ducklings are shown by dashed lines in Figure 4.

I assume that the patterns of intraintestinal HSD in ducklings will gradually change to those of the adults. For this to occur there must be a damping of diversity in the mid-region of the intestine and an increase in diversity in the anterior region of the intestine. There appears to be little change required in the posterior part of the intestine except for a moderate increase in the number of species.

Intraintestinal Helminth Distributions

In the examination of species distributions along resource gradients there are several parameters of these distributions that are of interest. One of the most important of these is shape. The simplest assumption concerning the shape of the distributions is that they are normal, bell-shaped ones. Therefore, the intraintestinal distributions of the populations of each of the dominant helminths in each adult or duckling was tested for normality by the Kolmogorov-Smirnov test. In no case did the distributions differ significantly from normality. However, populations of *F. fasciolaris* and *H. pusilla* did appear to be truncated at the anterior and posterior ends of the intestine respectively. In addition,

Table 9. Analysis of variance of measures of helminth species diversity between equal five-percent sections of the small intestines of 43 lesser scaup ducklings (% = percent of variance accounted for by regression)

Source	Species			Shannon diversity			Equitability			Simpson's Index		
	SS	F	%	SS	F	%	SS	F	%	SS	F	%
Regression	16.617	57.297***	.915	.925	55.249***	.912	.464	12.827***	.707	2.287	50.154***	.904
Linear	2.831	29.283***	.156	.164	29.407***	.162	.176	14.614**	.268	.530	34.898***	.209
Quadratic	12.848	132.896***	.707	.698	125.053***	.688	.282	23.424***	.430	1.712	112.642***	.677
Cubic	.939	9.711**	.052	.063	11.287**	.062	.005		.008	.044		.017
Error	1.547			.089			.192			.243		

** = p<.01

*** = p<.001

distributions of some other species appeared to be truncated at the ends of contact with certain other species. The latter will be covered more extensively in the section on interspecific interactions.

Since these distributions are essentially normal, three additional parameters are of interest: location, dispersion and kurtosis. In the following, the median point of distribution (i.e. location of the median individual of a population, abbreviated MP) will be used as an index of location, the range (R) as an indicator of dispersion, and Culver's (1972) measure of niche breadth (B) as a measure of kurtosis.

The dominant helminths of adult scaup occupied characteristic locations along the small intestine. The median points of each species were normally distributed and had remarkably low variance (Table 10). This is a very important feature of the intestinal helminth community of scaup. Because of this, species were found in characteristic sequences and each species was associated with a characteristic group of other species. The locations of the dominant species in individual birds appeared to be independent of their population size in those birds; in no case was MP significantly correlated with N.

Diorchotaenia coronula had the greatest variance in MP. This variance may be somewhat misleading. This is a large worm often spanning several sections; its location was taken as the location of the scolex. If I had used biomass as a measure of location this variance may well have been reduced.

End points of distribution were also fairly consistent within species, and showed approximately the same variances as MP (Table 10). However, the ranges within each species appeared to be somewhat more

Table 10. Intraintestinal distributions (means ± SD) of the dominant species of helminths from 30 adult lesser scaup

Helminth species	n	N	Median point	End points distribution	Range	Niche breadth (B)
Fimbriaria fasciolaris	30	194± 316	8± 4	0 -19± 8	19± 8	.30±.16
Lateriporus skrjabini	18	37± 51	19± 8	11± 9-28± 9	18±11	.24±.16
Hymenolepis recurvata	12	320± 521	24±11	10± 9-36±14	27±17	.35±.22
H. microskrjabini	17	2419±7145	27±11	15±12-40±11	25±15	.41±.26
H. spinocirrosa	29	7609±6806	37±14	18±13-58± 9	39±14	.53±.08
Retinometra pittalugai	23	715±1616	40±11	27±14-54±15	27±22	.35±.27
H. tuvensis	25	1218±2316	48± 8	35±10-61±11	25±14	.36±.18
H. abortiva	29	5077±5254	64± 8	51± 6-84± 9	30±13	.48±.11
Polymorphus marilis	30	60± 76	66± 6	51± 8-85± 8	33±12	.41±.21
Dicranotaenia coronula	14	27± 27	73±21	70±10-89±11	18±10	.29±.19
H. pusilla	28	2871±4081	90± 4	76± 7-99± 1	22± 9	.39±.12

variable. Between species the ranges appeared to be fairly consistent, with most species occupying 20 to 30 percent of the intestine. There was a tendency for species located at the ends of the intestine to have somewhat smaller ranges; otherwise, there were no correlations of range with location. What the range is dependant upon is population size. For most species there was a significant correlation between R and N (Table 11). Amongst the hymenolepidids, *H. spinocirrosa* and *H. abortiva*, the species with the greatest numbers, had the largest mean R.

Niche breadth, the measure of kurtosis (or a measure of evenness of distribution), showed considerable variability both within and between species. It showed no correlation with MP, but was usually significantly correlated with N, R or both. There was no change in niche breadth (or in location or range) due to season or year in any of the dominant species.

These observations indicate that in adult scaup each species of helminth occupies a predictable location along the intestine and as the size of their populations increase, individuals are dispersed evenly from their optimal points.

In ducklings as well, the dominant species occupy characteristic locations. Although the general region of the intestine occupied does not change, there were significant variations in MP with age in most of the dominant helminths (Table 12). Four species, *F. fasciolaris*, *H. albertensis*, *H. spinocirrosa* and *H. tuvensis* showed no significant change with age. Three other species, *H. abortiva* ($F = 8.63$, $p < .01$), *H. pusilla* ($F = 4.81$, $p < .05$) and *D. coronula* ($F = 5.27$, $p < .01$),

Table 11. Intercorrelations of ranges occupied (R), population sizes (N), and evenness of distribution (B) of the dominant species of intestinal helminths of adult scaup

Helminth species	R^a/N^b	B/N	B/R
Fimbriaria fasciolaris	.15	-.06	.23
Lateriporus skrjabini	.20	.75***	.40
Hymenolepis recurvata	.42	-.02	-.11
H. microskrjabini	.63**	.36	.85***
H. spinocirrosa	.52**	.52**	.81***
Retinometra pittalugai	.69***	.01	.07
H. tuvensis	.58***	.50**	.91***
H. abortiva	.60***	.67***	.85***
Polymorphus marilis	.62***	.42*	.88***
Dicranotaenia coronula	.88***	.75**	.94***
H. pusilla	-.06	.61***	-.09

* = $p < .05$

** = $p < .01$

*** = $p < .001$

a = dependent variable

b = independent variable

Table 12. Intraintestinal distributions (means ± SD) of the dominant species of helminths from 46 lesser scaup ducklings. (Mean values are shown only for those that show no significant difference between ages.)

Helminth species	Host age	n	N	Median point	End points distribution		Range	Niche breadth (B)
Pimbriaria fasciolaris	I_a	5	81± 57	14± 3	0	43±16	43±16	.57±.11
	I_b	10	70± 66	13± 3	2± 3	35±11	31±14	.52±.06
	I_c	10	90± 70	9± 3	1± 2	31± 5	31± 6	.51±.06
	II_a	8	124± 75	11± 3	0	33± 4	33± 4	.53±.06
	II_b	8	89± 40	9± 4	0	29± 7	29± 7	.44±.09
	$\bar{x}$			11± 3	.6± 1		33± 9	.51±.08
Hymenolepis fausti	I_a	0	-	-	-	-	-	-
	I_b	2	20± 25	63± 7	55±14	70± 0	15±14	.23±.32
	I_c	0	-	-	-	-	-	-
	II_a	2	80± 112	13± 7	3± 4	25±21	23±25	.33±.47
	II_b*	6	703± 648	53±29	18±33	71±29	53±34	.51±.30
	$\bar{x}$							
Lateriporus skrjabini	I_a	3	3± 1	26± 3	15± 9	32± 6	17± 3	.25±.08
	I_b	1	2	8	5	10	5	0
	I_c	6	6± 8	23± 6	19± 6	33± 6	13± 8	.18±.20
	II_a	6	9± 9	23±10	18± 7	34±12	16± 7	.25±.14
	II_b	7	29± 37	30±10	23± 9	37±12	14±10	.21±.19
	$\bar{x}$				16± 7	29± 7	13± 7	.18±.14
H. microskrjabini	I_a	5	102± 79	27± 7	13±10	43± 8	30±13	.45±.12
	I_b	8	75± 94	22± 5	8± 7	33± 8	24±12	.39±.11
	I_c	11	428± 653	30± 5	12± 7	43± 8	31±12	.41±.11
	II_a	8	287± 256	26± 7	7± 8	40± 6	31± 6	.43±.09
	II_b	8	616± 565	34± 5	14± 6	45± 6	30±11	.35±.11
	$\bar{x}$				11± 8	41± 7		.41±.10
H. albertensis	I_a	5	234± 153	38± 5	9±13	53± 8	44±13	.55±.08
	I_b	9	139± 175	36± 6	14±17	49± 8	32±19	.27±.15
	I_c	8	209± 158	34±12	16±13	50±10	34±14	.38±.08
	II_a	7	120± 138	37± 4	17±15	47±10	30±23	.31±.18
	II_b	5	160± 186	37± 4	30± 4	45± 6	15± 6	.24±.13
	$\bar{x}$			36± 6		49± 7		
H. spinocirrosa	I_a	5	438± 426	45± 3	27± 3	60±12	33±12	.48±.21
	I_b	9	1350±1077	40± 6	13± 9	73±18	60±19	.60±.04
	I_c	11	669± 419	42± 3	25± 9	59± 7	31±11	.43±.09
	II_a	8	1784± 897	42± 3	25± 8	69±11	41±20	.54±.07
	II_b	8	1680±1952	44± 4	29±11	61±11	32±15	.36±.16
	$\bar{x}$			43± 4	24± 8	64±12	39±15	.48±.11

Table 12 (continued)

Helminth species	Host age	n	N	Median point	End points distribution		Range	Niche breadth (B)
H. tuvensis	I_a	5	38± 32	47± 7	33± 5	58±13	25±13	.39±.23
	I_b	6	50± 43	37±11	26±14	51±10	25±13	.27±.13
	I_c	11	137± 173	42± 7	34±10	53±14	23±14	.34±.22
	II_a	8	284± 125	39± 5	28± 5	61±10	33±14	.39±.08
	II_b	8	540± 473	42± 5	30±11	61± 7	32±13	.42±.08
	$\bar{X}$			41± 7	30± 8	57±11	28±13	.36±.11
H. abortiva	I_a	2	39± 27	70± 4	68± 4	85± 7	18±11	.14±.10
	I_b	9	76± 58	59± 3	51± 4	73± 6	22± 8	.39±.11
	I_c	9	155± 214	58± 8	51± 6	71± 9	20±10	.34±.12
	II_a	7	200± 168	58± 2	51± 4	74± 5	24± 6	.42±.15
	II_b	7	448± 302	58± 4	51± 2	71± 9	20± 8	.32±.11
	$\bar{X}$				54± 4	75± 8	21± 9	.32±.12
Polymorphus marilis	I_a	2	1± 0	75±11	73±11	78±11	5± 0	0
	I_b	6	4± 3	76± 8	68±11	82± 9	13±11	.24±.16
	I_c	8	5± 6	63±11	58± 9	73±12	15±10	.22±.16
	II_a	7	3± 2	66± 8	61± 9	72± 8	11± 5	.23±.08
	II_b	10	12± 13	72± 9	61± 9	83±10	23± 9	.34±.13
	$\bar{X}$				64± 9	78±10	13± 7	.21±.15
Dioranotaenia coronula	I_a	2	3± 1	71± 5	63± 4	85± 0	23± 4	.30±.10
	I_b	4	2± 2	73± 9	69±11	78± 7	9± 8	.12±.23
	I_c	5	3± 1	63±13	58±14	75±13	17±14	.23±.15
	II_a	6	3± 3	69±15	62±14	81±11	19±18	.17±.15
	II_b	7	8± 7	52±20	37± 9	78±14	28±16	.28±.18
	$\bar{X}$				58±10	79± 9	19±12	
H. pusilla	I_a	4	49± 31	79± 8	61± 6	96± 5	35± 9	.52±.09
	I_b	9	69± 71	78± 5	65± 5	91± 7	21±15	.43±.09
	I_c	11	154± 130	77± 7	62± 9	95± 6	25±16	.48±.12
	II_a	8	236± 103	78± 3	64± 6	98± 4	34± 5	.50±.05
	II_b	8	326± 157	84±10	63± 6	98± 4	36± 4	.50±.06
	$\bar{X}$				63± 6	96± 5	30±10	.49±.08

*Includes 4 ducklings with unusually high population of *H. faloti*

showed apparent directional movements. *Hymenolepis abortiva* and *D. coronula* were located progressively more anteriorly while *H. pusilla* was located more posteriorly. The other species, *H. microskrjabini*, *L. skrjabini* and *P. marilis*, showed significant variations ($p < .05$) between age classes, but these changes appeared to reflect jostling rather than any directional movement. In no case was there a significant correlation between MP and N.

The ranges and end points of distributions of the dominant helminths of ducklings were fairly consistent within species. *Hymenolepis albertensis* was the only species whose range changed significantly with age of host. In the Ia ducklings it occupied 44 percent of the intestine, but, by the IIb age category, its range had decreased to 15 percent. Despite this reduction in range there were no differences in location or posterior end point; the restriction appeared to be due solely to a restriction of the anterior end point. This decrease in range was not correlated with a statistically significant decrease in population size.

There were few significant correlations between range of a particular dominant helminth in an individual duckling and its population size in that duckling. However, this analysis compared ducklings of very different sizes. To account for these differences, the number of worms was divided by the length of the intestine. The resulting adjusted population sizes ($\bar{N}$/cm) were significantly correlated with range for all dominant helminths except *H. fausti* and *H. tuvensis* (Table 13).

Once again, niche breadth showed considerable variability within and between species. It showed no correlation with MP but was usually

Table 13. Intercorrelations of ranges occupied (R), populations sizes(N), and evenness of distribution (B) of the dominant species of intestinal helminths of scaup ducklings.

Helminth species	R^a/N^b r	$R/\frac{\bar{N}}{cm}$ r	B/N r	$B/\frac{\bar{N}}{cm}$ r	B/R r
Fimbriaria fasciolaris	.21	.50**	.28	.33*	.89***
Hymenolepis fausti	.07	.08	.13	.06	.12
Lateriporus skrjabini	.58*	.56***	-.12	.69***	-.27
H. microskrjabini	.09	.37*	-.02	.27	.89***
H. albertensis	.39	.62***	.34	.38*	-.29
H. spinocirrosa	.22	.46*	.17	.43*	.86***
H. tuvensis	.05	.21	.14	.31*	.90***
H. abortiva	.05	.40*	-.01	.17	.66**
Polymorphus marilis	.52*	.57***	-.02	.38*	.26
Dicranotaenia coronula	.57**	.76***	.49	.57**	.35
H. pusilla	.27	.64***	.19	.02	.92***

a = dependent variable
b = independent variable
* = $p<.05$
** = $p<.01$
*** = $p<.001$

significantly correlated with $\bar{N}$/cm (but not N), R or both.

It is apparent that the dominant species occupy the same general region of the small intestine in both adults and duckling scaup. The median points of *H. microskrjabini* and *H. spinocirrosa* did not differ significantly in the two groups. In addition, the location of *R. pittalugai* (in adults) was indistinguishable from that of *H. albertensis* (in ducklings); this provides additional evidence for their being ecological equivalents. Other species showed significant differences in MP between ducklings and adults, as might be expected considering the changing distributions in ducklings. When the distributions of the dominant helminths of adults were compared with those of the oldest ducklings (IIb), there were no significant differences in MP. It would appear that these changes in location in ducklings represent ontogenetic adjustments leading to the normal pattern of distribution in adult scaup.

Essentially the same processes appear to be operative with the ranges of some species. *Hymenolepis abortiva* and *P. marilis* have smaller ranges in ducklings than adults, as might be expected from their markedly smaller population sizes. *Fimbriaria fasciolaris* and *H. pusilla*, located at the ends of the intestine, have much larger ranges in ducklings than in adults. The process of compressing the distributions of these species does not appear to be complete in ducklings of this age.

Hymenolepis fausti was the only species that did not show a consistent, characteristic location. In adults and in two IIa ducklings (Table 12), it occupied a narrow range in the anterior region of the intestine. However, in two Ib ducklings it was found in a narrow range

just posterior to the middle of the intestine. In six IIb ducklings its population sizes and ranges occupied were variable, including some ducklings in which it was distributed virtually throughout the intestine. In these extreme cases the other dominant species were essentially absent. These cases will be considered further in the following section.

Interspecific Interactions

The sequential distributions of species along the small intestine are the most interesting aspects of the helminth community of scaup, since they raise the question: *To what extent are they due to interactive segregation?* (Holmes 1973). The answer to that question is difficult to obtain from field data. Several analytical approaches, such as recurrent group analysis (Fager 1957) and TAXMAP cluster analysis (Carmichael and Sneath 1969); a variety of manual sorting techniques, such as dendograms and constellation diagrams; and various statistical analyses, such as multiple regression techniques, correlation matrices and analysis of covariance, were used in attempts at initial screening. The results were not particularly useful.

As an alternate approach the habitat niche overlaps (HNO) (as measured by percent similarity (PS) of distribution, see p 9) between the dominant species of intestinal helminths of adult scaup were organized into a trellis diagram (Macfadyen 1964) (Table 14). As expected from the general pattern of distribution (Table 10) each species shows the greatest overlap with adjacent species. In addition the data showed four overlapping groups of species in adult scaup (these groups are blocked off in Table 14), with moderately high overlap values within each group and relatively low overlap values between species not in the same group.

Table 14. Habitat niche overlaps (mean percent similarity ± standard deviation) for the dominant species of helminths of adult lesser scaup.

Helminth species	Hr	Ls	Hm	Rp	Hs	Ht	Ha	Pm	Dc	Hp
Fimbriaria fasciolaris	16±21	17±18	13±25	2± 4	4± 6	0	0	0	0	0
Hymenolepis recurvata		32±38	8±23	9±20	10±12	4±11	1± 4	0	0	0
Lateriporus skrjabini			29±29	12±19	13±18	11±15	0	0	0	0
H. microskrjabini				16±21	12± 9*	12±13	1± 4	0	0	0
Retinometra pittalugai					36±24	24±21	11±12	6± 9	0	0
H. spinocirrosa						40±27	6± 4	5± 9	4± 3	0
H. tuvensis							18±22	13±17	7± 4	0
H. abortiva								57±16	16±15	2± 4
Polymorphus marilis									19±10	9±12
Dicranotaenia coronula										21±13
H. pusilla										

*significant linear increase in overlap with season ($p<.05$)

Identification of such groups allows one to focus attention on the most likely places and species to find interactions. Within each group most of the species overlapped broadly (i.e., HNO 15 or more), so that their niches must be separated on dimensions other than the spatial one (represents 24 percent of the HNO's). Low HNO's (i.e., less than 15) between species in the same group (11 percent of the HNO's) might be explicable on two quite different grounds; the species may be located at opposite ends of the groups or they may show strong negative interactions. The only cases in which the two species were not at opposite ends, thus suggesting negative interactions, were *H. microskrjabini* with *H. recurvata* or *H. spinocirrosa*. *Hymenolepis microskrjabini* and *H. recurvata* occupy essentially the same region of the intestine (Table 10), but show very little overlap (Table 14). *Hymenolepis microskrjabini* and *H. spinocirrosa* occupy somewhat different parts of the intestine (Table 10) and show relatively low overlap; however, their overlap was the only one that showed a significant increase throughout the summer. The relationships between these three species will be considered in more detail later in this section.

The remainder of the HNO's in Table 14 can be divided into two groups. First, species which do not overlap, so that any interactions between them must be mediated through the host (35 percent of HNO's). Covariance analyses gave no evidence for such interactions. Second, species with low to moderate overlaps (HNO's 1-15); although there may be interactive segregation between such species, most appear to be separated by preferred location.

In a second effort to screen the data for interactions between species,

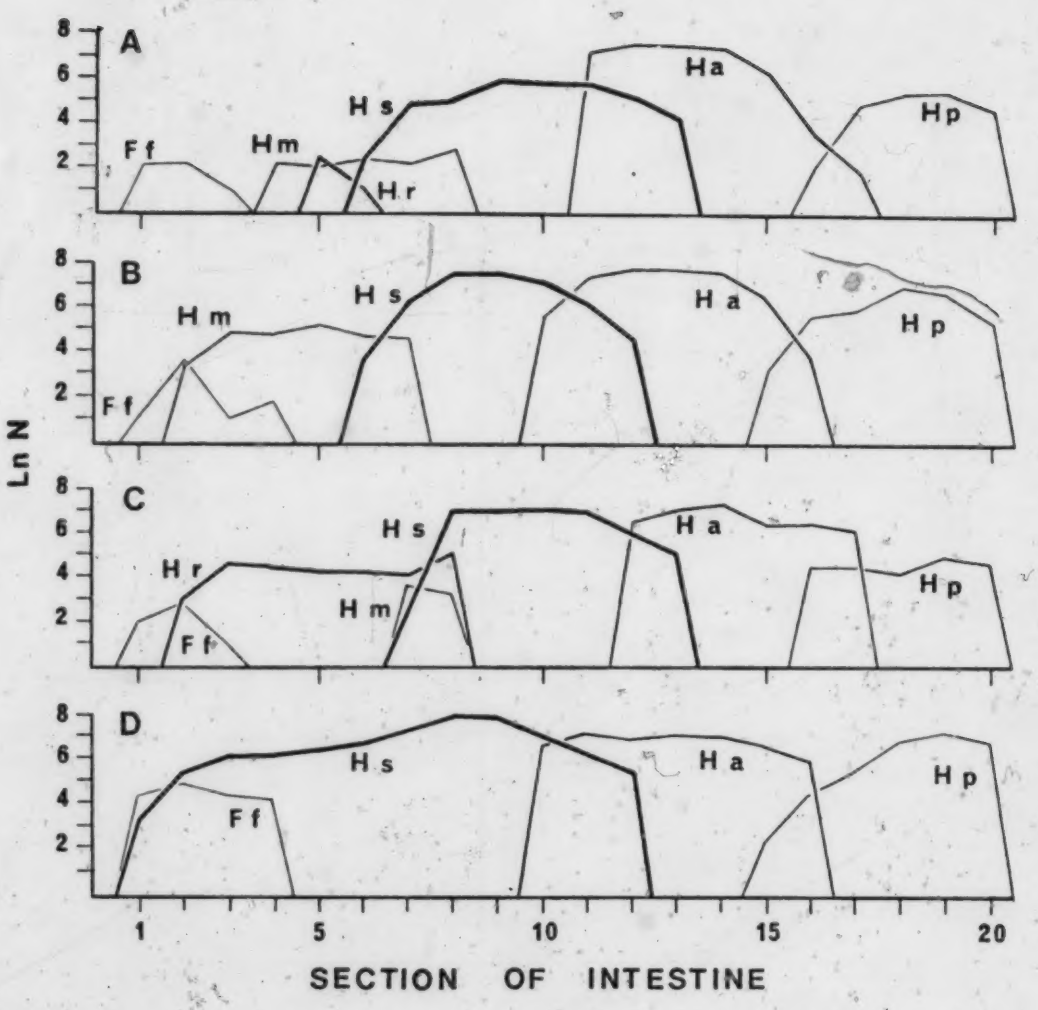
the HNO's, at the level of the host individual, were grouped into: (a) those which did not differ significantly from mean values, the "characteristic" values, and (b) those which differed significantly from the mean values, the "displaced interactions." Data from birds with HNO's in the two groups were then screened for significant differences in faunal composition, relative abundances, median points and/or end points of distribution. Although over 20 sets of "characteristic" and "displaced" groups were screened, the only species in which the end points of distribution differed significantly were *H. microskrjabini*, *H. recurvata*, and *H. spinocirrosa*. There were no interpretable differences in relative abundances or location.

Both screening procedures suggested that interactions between *H. microskrjabini*, *H. recurvata*, and *H. spinocirrosa* were particularly important. Focusing on interactions between these three species, the communities in 26 of the 30 adult scaup could be placed into one of the following four categories:

(A) All of the dominant species were present and characteristically distributed, but their population sizes were relatively low. Figure 5A shows the distributions and populations of three indicator species, *F. fasciolaris*, *H. abortiva*, *H. pusilla*, and the three species of particular interest in five adult scaup. The distributions shown in Figure 5 are the mean numbers per infected bird for each section of the intestine. Variations in these distributions and the distributions of the other dominant species are given in Appendix IV.

(B) Particularly high populations of *H. microskrjabini*; *H. recurvata* (which occupies the same region of the intestine) was absent or in low

Figure 5. Alternate patterns in the structure of the intestinal helminth community of adult lesser scaup (see text for explanation; Ff = *Fimbriaria fasciolaris*, Hf = *Hymenolepis fausti*, Ha = *H. abortiva*, Hm = *H. microskrjabini*, Hp = *H. pusilla*, Hr = *H. recurvata*, Hs = *H. spinocirrosa*).


A
B
C
D
Ff
Hm
Hr
Hs
Ha
Hp
8
6
4
2
Ln N
1
5
10
15
20
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numbers; other species relatively abundant and characteristically distributed (five adult scaup; Figure 5B).

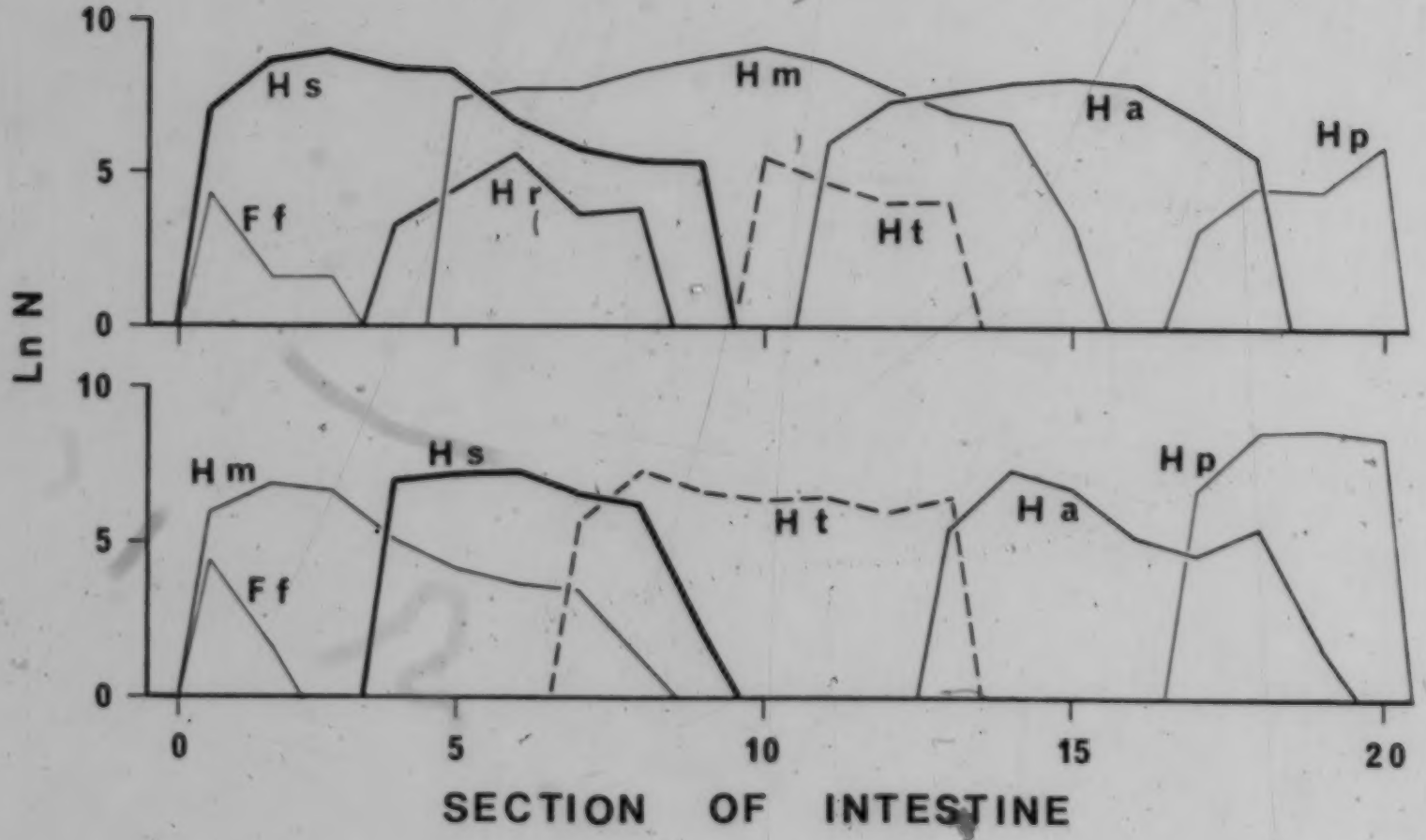
(C) *Hymenolepis recurvata* high; *L. skrjabini* absent; *H. microskrjabini* absent or in low numbers; other species relatively abundant and characteristically distributed (three adult scaup; Figure 5C).

(D) *Hymenolepis microskrjabini* and *H. recurvata* absent or in very low numbers, with a significant ($p < .001$) anterior extension of the distribution of *H. spinocirrosa*; other species relatively abundant and characteristically distributed (12 adult scaup; Figure 5D). It should be noted that eight of the ten birds taken in August fell into this group.

The four adult scaup that were not included in these categories were two birds which lacked either *H. spinocirrosa* or *H. abortiva*, but were otherwise similar to those in the first category, and two other scaup in which the populations of *H. spinocirrosa* and *H. abortiva* were displaced, nonoverlapping, and separated by large populations of *H. tuvensis* or *H. microskrjabini* (Fig. 6). The latter two cases suggest that the characteristic patterns of community structure can be altered by high populations of certain species.

The same kinds of analyses were performed on data from ducklings as on those from adults. Although in ducklings the HNO's between the dominant species showed three overlapping groups of species (Table 15) as opposed to four in adults, groupings of species were essentially the same in adults and ducklings. Two relatively minor differences were the absence in ducklings of *H. recurvata*, a member of the most anterior group in adults, and the replacement of *R. pittalugai* by its

Figure 6. Effects of high populations of *Hymenolepis microskrjabini* and *H. tuvensis* on the patterns of intraintestinal distributions of the other dominant helminths of adult lesser scaup (see Figure 5 for key to species).


10
5
0
Ln N
Hs
Hm
Ha
Hp
Ff
Hr
Ht
10
5
0
Hm
Hs
Ht
Ha
Hp
Ff
0
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10
15
20
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Table 15. Habitat niche overlaps (mean percent similarity ± standard deviation) for the dominant species of helminths of lesser scaup ducklings.

Helminth species	Ff	Ls	Hm	Halb	Hs	Ht	Ha	Pm	Dc	Hp
Hymenolepis fausti	13± 6	4± 5	8± 4	5± 3	0	4± 3	3± 2	2± 2	0	0
Fimbriaria fasciolaris		15±11	23±14**	8± 9	4± 6	4±10	0	0	0	0
Lateriporus skrjabini			36±26	15±16	12±14	11±16	0	0	7±14	0
H. microskrjabini				29±22	21±17	23±22	0	0	5± 8*	0
H. albertensis					44±21	48±28	1± 1	0	6±17*	0
H. spinocirrosa						52±23	9± 8	4± 8	13±22*	0
H. tuvensis							4± 5	5± 9	6±11	2± 5
H. abortiva								20±23	16±20	7±6**
Polymorphus marilis									11±18	20±18
Dicranotaenia coronula										21±17
H. pusilla										

*significant linear increase in overlap with age of host ($p<.05$).
**significant linear decrease in overlap with age of host ($p<.05$).

ecological equivalent in ducklings, *H. albertensis*, in the second group. More important differences were the lower HNO's between *H. tuvensis* and *H. abortiva* or *P. marilis*, and the greater overlap between *P. marilis* and *H. pusilla*. These latter differences appear due to the more restricted ranges of *H. abortiva* and *P. marilis*, and the greater range of *H. pusilla*, in ducklings.

There were a number of significant linear regressions of HNO on age of host. These are indicated by asterisks in Table 15. The decrease in overlap between *F. fasciolaris* and *H. microskrjabini* can be accounted for by the decrease in importance of *H. albertensis* in older ducklings, which permitted *H. microskrjabini* to occupy its characteristic location somewhat more posterior. The mature *D. coronula* in older ducklings were more anterior, thereby increasing overlap with *H. albertensis*, *H. microskrjabini* and *H. spinocirrosa*. *Hymenolepis pusilla* moved posterior with age resulting in a decrease in overlap with *H. abortiva*.

The data from ducklings were screened by the same methods as those from adults. No interesting examples of interactions were found. Of the interesting triad in adults, only two (*H. microskrjabini* and *H. spinocirrosa*) were present in ducklings. Their interactions in ducklings were fairly consistent.

By the time the helminth community was established in the oldest age category of ducklings (IIb), the overlaps and end points of distribution of the dominant helminths were not significantly different from those of adult scaup. At this time the distribution of species resembled those in Figure 5B. A comparison of the distributions of the species in this age class of duckling (Table 12) with those in

group B (Appendix IV) shows an increase in range of *F. fasciolaris* and *D. coronula*, and the previously mentioned decreased range of *H. abortiva* and *P. marilis*. Otherwise differences are inconsequential.

However, the IIb ducklings analyzed above do not include three ducklings that had high numbers of *H. fausti*. This species was generally present in low numbers and was usually distributed in the anteriormost region of the intestine, as in Figure 7A. However, at higher population levels its range extended significantly posteriorly (Figure 7B,C,D). In two ducklings with the highest numbers of *H. fausti*, the rest of the helminth community was essentially absent. The interpretation of this is unclear but the possible purturbating effects of *H. fausti* are of particular interest and merit further research.

One of the major difficulties in interpreting multi-species interactions is the complete lack of information on distributions in single species infections. A limited number of observations were made on experimental and/or naturally acquired single species infections of *H. abortiva* and *H. spinocirrosa*. These distributions are shown in Figure 8. *Hymenolepis abortiva* is normally located posterior to *H. spinocirrosa* (Fig. 5) with a relatively low degree of overlap (Tables 14 and 15). In single species infections, although the populations were lower, the end and median points of distribution of *H. spinocirrosa* (five observations) were not significantly different than they were in multi-species infections. However, *H. abortiva* (one observation) was distributed somewhat anterior to its normal location, in essentially the same location as *H. spinocirrosa*. In a single experimental

Figure 7. Effects of different population levels of *Hymenolepis fausti* on the helminth communities of individual lesser scaup ducklings (see Figure 5 for key to species).

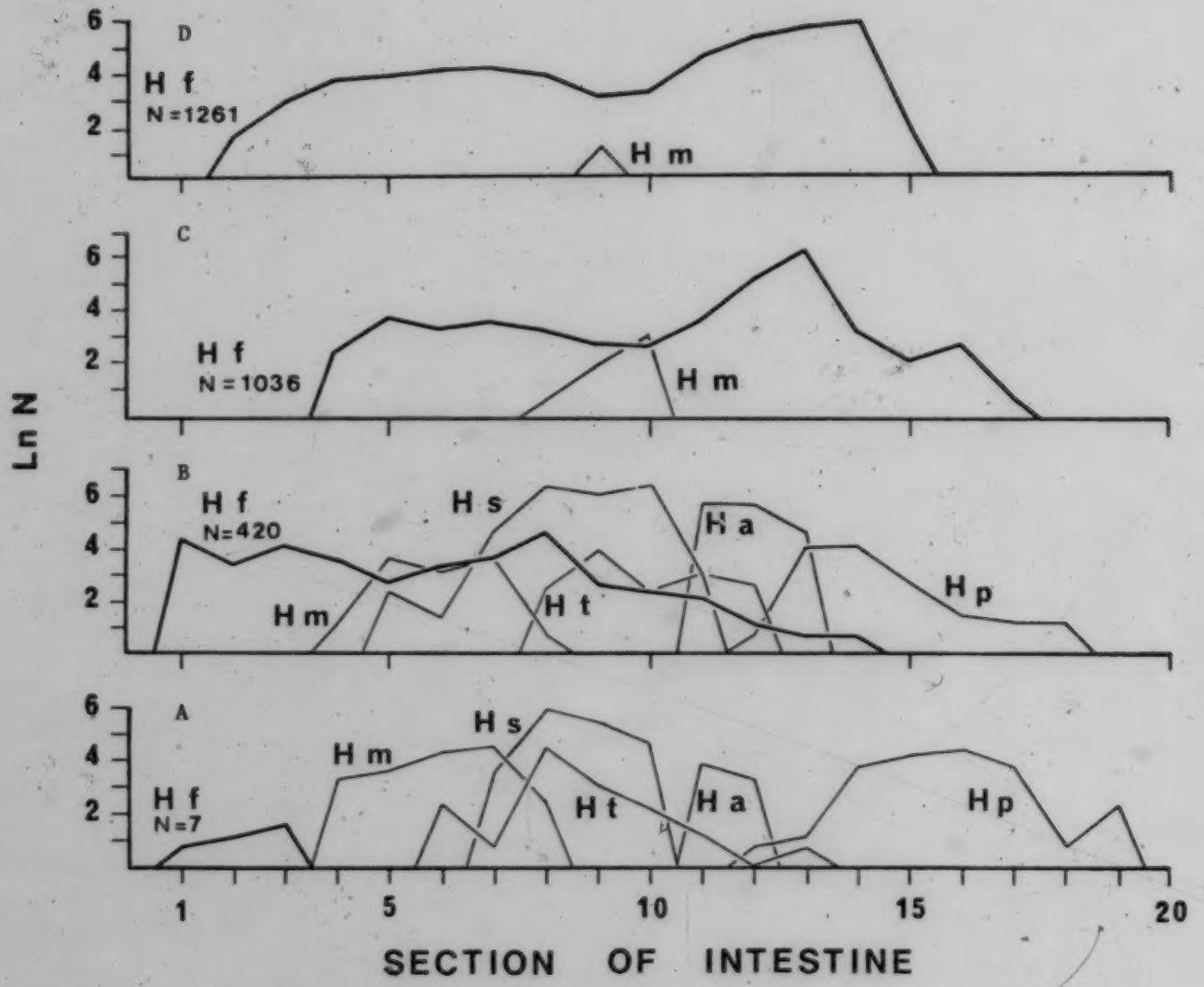
D
H f
N=1261
H m
C
H f
N=1036
H m
B
H f
N=420
H s
H a
H p
H m
H t
A
H s
H m
H f
N=7
H t
H a
H p
6
4
2
Ln N
1
5
10
15
20
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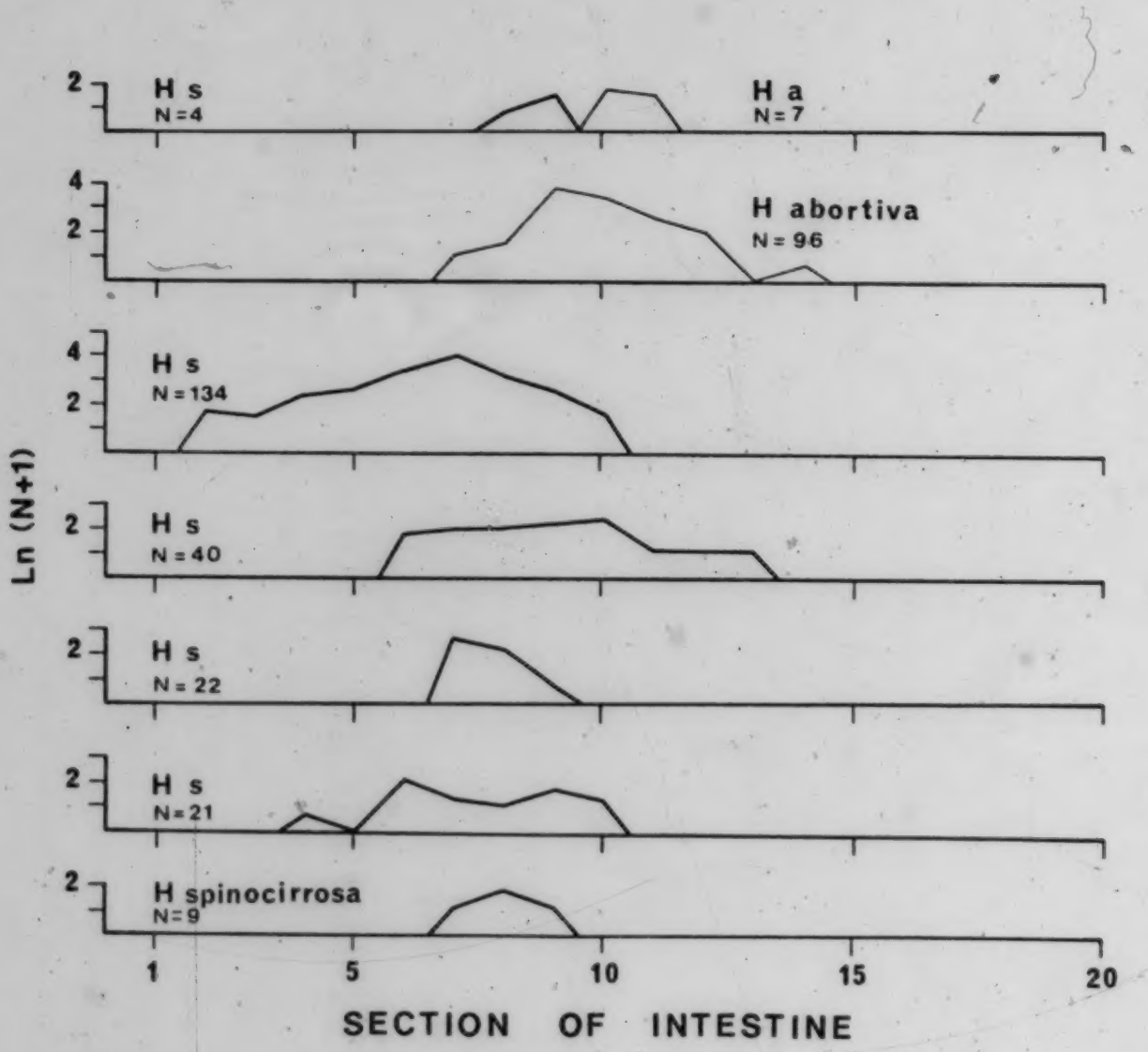
Figure 8. Distribution of *Hymenolepis spinocirrosa* and *H. abortiva* in single and concurrent infections.


H s
N=4
H a
N=7
H abortiva
N=96
H s
N=134
H s
N=40
H s
N=22
H s
N=21
H spinocirrosa
N=9
Ln (N+1)
SECTION OF INTESTINE

concurrent infection with these two species only, the small numbers of each present occupied abutting ranges.

Discussion

The material presented above has clearly demonstrated that spatial factors, specifically different intraintestinal distributions of the dominant helminths, are of major importance to the community of helminths in scaup. The most striking feature of the data is the remarkable consistency in composition and locations of the dominant species of helminths in different scaup. Although this feature was most marked in the adults (which represent the fully developed community), it was also apparent in the data from ducklings as young as one week old.

Although there appear to be no studies in which the consistency in location of individual species of helminths in individual birds has been demonstrated statistically, Avery (1969), Czaplinski (1973), Olszewska (1973) and Stradowski (1973a,b) all comment on the consistency of location of the hymenolepidids they studied in various species of waterfowl.

At least some helminths appear to show consistent intraintestinal locations in studies from different geographical regions and/or different hosts. The most obvious example is *D. coronula*. Crompton and Harrison (1965) and Avery (1969) reported it from the posterior part of the small intestine of mallards in England. This is the same general location that it occupied in scaup. In addition, Avery (1969) reported *F. fasciolaris* from the anterior

region of the small intestine, the same region as in my study. However, Whitfield (in Crompton 1973) reported this species from the posterior part of the intestine of "ducks". This difference may be due to post-mortem migration, since I have observed a posteriad movement of this species in birds whose intestines were not frozen in the field.

There are other species in which different studies have reported different locations. *Hymenolepis fausti* was reported from the caeca of black ducks (*A. rubripes*) by Schiller (1951). In my study its location was variable but it was never found in the caeca. Similarly, *H. abortiva* has been reported from the caeca of mallards (Wisniewski *et al.* 1958) and black ducks (McLaughlin and Burt 1973), but in my study it was found between the 51 and 84 percent points. These observations may be interpreted in one of two ways: either subpopulations of the same species have different locations in different hosts, or helminths identified as the same species are in fact not the same.

A less radical change in location has been reported for *Diorchis stefanskii*. Avery (1969) reported it from the posterior end of the intestine, in essentially the same location as *D. coronula*. In contrast, Stradowski (1973a,b) reported that this species was found predominately in the second half of the jejunum and the first half of the ileum. However, it should be noted that Avery was dealing with naturally acquired, multi-species infections, whereas Stradowski was working with experimental single species infections.

When the distributions of the individual species reported in this study were compared, it was apparent that they were independent

and overlapping. There were few cases where the endpoints of distribution of different species coincided and none of these involved a sufficient number of species to suggest a discontinuity in the intestinal gradient. There were individual ducks in which pairs of species showed truncated, abutting distributions, but in other ducks the same species showed moderate overlaps.

In an important theoretical paper, Terborgh (1971) outlined three models to explain the limits on the distribution of species along environmental gradients. The models state that the occurrence of species is limited by (1) physical or biological conditions that vary in parallel with the measured gradient, ("Gradient" model) (2) competitive exclusion ("Competition" model) and (3) environmental discontinuities ("Ecotone" model). Table 16 (Terborgh's Table 1) lists the predictions of these models. In his terminology "amplitude" indicates the species range along the gradient, a "terminus" is an arbitrary end point along a continuing gradient and a "congruity curve" is a measure of the rate of change of species along the gradient (for details see Terborgh 1971). Since the termini in my study are not arbitrary points, but represent major discontinuities in the digestive tract, the last prediction does not apply.

It is apparent that my data agree with the rest of the predictions for the gradient model. This agreement supports the hypothesis that each species of intestinal helminth is genetically adapted to the conditions of a specific location in the intestine and therefore, that selective segregation (Nilsson 1967) is an

Table 16. Predictions of three models of species distribution on environmental gradients. Predictions unique to the given model are in italics (Table 1 in Terborgh 1971)

Distributional feature	Model: Gradient	Competition	Ecotone
1. Population density curve	± normal	*repulsion interaction*	*truncation*
2. Mutual exclusion	none	*yes*	none
3. Amplitude compression	none	*yes*	none
4. Congruity curves	smooth, symmetrical	smooth, symmetrical	*discontinuous*
5. Amplitude distribution curve	± normal	*skewed right*	variable
6. No species near terminus	*reduced*	not reduced	not reduced
7. Species loss near terminus	*not reduced*	reduced	reduced
8. Species gain near terminus	reduced	reduced	reduced
9. Mean amplitude near terminus	*reduced*	constant	constant

important factor in determining the complexity of the community of intestinal helminths in scaup. These conclusions suggest that the species of intestinal helminths in scaup have progressed a considerable distance along the evolutionary sequence from interactive segregation to selective segregation outlined in Holmes (1973). They further support the hypothesis that the community of intestinal helminths in lesser scaup is a mature one, whose diversity has been established to an important extent through biotic interactions.

Communities in other waterfowl may show the same general features. Avery (1969) found that each of seven species of tapeworms in mallards occupied a characteristic zone of the alimentary canal and that they formed a sequence of overlapping populations. He presented this sequence diagrammatically. Czaplinski (1973) divided the intestines of swans (*Cygnus olor*) into six sections, and found that each of the six species of hymenolepidids that matured and were reasonably common was most abundant in a specific section and was present, but less abundant, in adjacent sections. Although the smaller number of species and methods of presenting the distributions of these species do not permit detailed comparison with Terborgh's (1971) predictions, the sequences of overlapping distributions certainly seem to favor the gradient model, and therefore the interpretations made for the community of intestinal helminths in scaup.

Although the preceding discussion has emphasized the importance of selective segregation, it should not be construed that interactive segregation does not occur. Although the examples were

fewer, and involved a small proportion of the species, they did occur. The most obvious example involved the three way interaction between *H. microakrjabini*, *H. recurvata* and *H. spinocirrosa*. All these species can occupy the region between the 10 and 40 percent points, but not concurrently. It would appear that moderate populations of *H. microakrjabini* and *H. recurvata* can co-occur, with no evidence of spatial segregation. However, high populations of *H. microakrjabini* or *H. recurvata* occurred only in the absence of the other. Either, or both, could apparently exclude *H. spinocirrosa*. In the August scaup, in which *H. recurvata* was absent and the prevalence of *H. microakrjabini* was low, *H. spinocirrosa* occupied this area of the intestine and attained high populations. None of these changes appeared to affect the distributions of any of the other dominant species, therefore, the effects on the structure of the community appear to be purely local.

One of these species, *H. microakrjabini*, appear to be involved in a second example of interactive segregation. In young ducklings, *H. albertensis* occupies a substantial portion of the small intestine, between the 9 and 56 percent points. In these ducklings, populations of *H. microakrjabini* were relatively low. The range of *H. albertensis* was progressively reduced through exclusion from the anterior portion until in the IIb ducklings the anterior end point was at the 32 percent mark. At the same time populations of *H. microakrjabini* increased and occupied this region of the intestine. When *H. albertensis* was absent, populations of *H. microakrjabini* were somewhat higher. In a previous section it was pointed out that *H.*

albertensis was an opportunistic species, replaced in adults by *R. pittalugai*. It appears to be replaced in ducklings by *H. microakrjabini*.

Less conclusive evidence is available for interactive segregation between *H. abortiva* and *H. spinocirrosa*. In the few single species infections, their ranges occupied overlapped broadly, but in multi-species infections their distributions overlapped only moderately, and in a few individual ducks they showed abutting distributions, similar to those Terborgh (1971) predicted for competitive exclusion.

The number of overlapping distributions in a section of the intestine and the relative abundance of the species occupying those distributions determine the diversity of the parasite community in that section. If it can be assumed from the preceding discussion that the helminth community of scaup is a mature one, and if the additional assumption is made that mature communities are saturated, then the diversity of the helminths in any section may indicate the diversity of available niches in that section. If so, it would appear that the diversity of niches decreases along the intestine of lesser scaup.

It must be emphasized that in this study, no attempts were made to determine the dimensions on which niches could be separated in an individual section. It is very likely that trophic dimensions are involved. On the basis of the work of Schad (1963), Wertheim (1970) and Inglis (1971), a radial dimension of the spatial component may also be involved. All of the parasites in this study attach to the mucosa, but there may be a differential location of the strobila or body of different worms, using the space between villi

or folds, rather than the central lumen. Observations on cross-sections from various locations along the small intestine of scaup indicated that the anterior region was obviously structurally more complex, suggesting there may be more spatial niches available in this region of the intestine.

The process of developing from a pioneering community in ducklings to a mature one, comparable to that of adults, is rapid. The dominant helminths, particularly those in the mid-region of the intestine (*H. abortiva*, *H. spinocirrosa*, *H. tuvensis*), attain high population levels in a short period of time. These features are important in producing the parabolic pattern of diversity in ducklings. As the community continues to develop, populations of other species are acquired and/or those already present increase in number. These are the important factors responsible for the damping effect on the pattern of diversity in the mid-region of the intestine and the increase in diversity in the anterior region.

VI. GENERAL DISCUSSION

Patterns of species diversity along resource gradients are generated by species replacing one another within or between habitats. Whittaker (1965) has termed the former "alpha diversity" the latter "beta diversity". MacArthur (1960) pointed out that within-habitat diversity must be understood before between-habitat diversity can be considered.

In a diversity gradient study such as mine, it is particularly desirable to partition the total diversity of the data into its component parts, so as to distinguish the extent to which the regulation of species diversity is at each level. If an individual scaup can be considered to be a unit of "habitat", two levels of within-habitat diversity (α_I and α_G) and two levels of between-habitat diversity (β_B and β_I) can be distinguished in my study. They are:

(1) α_I is the base diversity or the average diversity within each section of the small intestine and may be considered to be the diversity associated with radial and/or trophic segregation.

(2) α_G is the additional diversity associated with combining sections within individual birds and may be considered to be the diversity associated with spatial segregation of species.

(3) β_B (adults) is the additional diversity associated with combining birds within samples taken at the same month and year, and may be considered to be the diversity associated with alternate communities in different birds taken at the same time. β_B (ducklings) is the additional diversity associated with

combining ducklings within age categories taken in the same year. This may be interpreted in the same way as β_B for adults.

(4) β_T is the additional diversity associated with combining adults or ducklings from different samples. It will include diversity due to temporal segregation, whether by year or season.

Given the additive properties of the Shannon formula (Pielou 1969; Allan 1975) it is possible to partition the total diversity of the helminth communities of scaup into these different levels of diversity. The contribution at each level can then be identified (Table 17).

In Table 17, the additional diversity associated with combining adults with ducklings was not included. There was one pair of species segregated between adults and ducklings and therefore, it is recognized that this would have a moderate effect on total community diversity. In the following analysis, these effects were considered to be relatively unimportant.

An examination of Table 17 indicates that overall, diversity associated with temporal segregation (β_T) was relatively unimportant in the intestinal community of scaup. The contribution at this level was slightly higher in ducklings than it was in adults (9 and 4 percent respectively). This is consistent with the moderately higher values of diversity indicated previously for ducklings.

The contribution of diversity associated with alternate communities (β_B) was similar for adults and ducklings (19 and 20 percent respectively). The relatively low contribution at this level is not particularly surprising since many of the important

Table 17. Partitioning of within and between habitat diversity for the intestinal helminth community of lesser scaup.

	Adults			Ducklings		
	Cumulative Mean (H´)*	Contribution	Percent	Cumulative Mean (H´)	Contribution	Percent
α_I (within section)	.39	.39	23	.46	.46	26
α_G (sections)	1.28	.89	54	1.26	.80	45
β_B (birds)	1.59	.31	19	1.62	.36	20
β_T (temporal)	1.66	.07	4	1.77	.15	9

H´ = Shannon diversity

features of the helminth community of scaup were remarkably consistent.

Intestinal parasites acquire nutrition by absorption of gut lumen contents and/or directly from host tissues. Aspects associated with trophic niche dimension were beyond the scope of this study. However, it is recognized that these features are important, particularly when one considers the distribution of diversity associated with the within section level (α_1) (approximately 25 percent for adults and ducklings). The helminths of scaup are habitat specialists and further research on their trophic relationships is warranted.

Without question, the most important features of this helminth community are those associated with spatial diversity. It accounts for approximately 50 percent of the diversity for the helminth communities of adults and ducklings. For the most part, it appears to be due to selective segregation by each species of parasite, with some modification due to interactive segregation. These conclusions support two important hypotheses:

(1) Spatial segregation is essential for the development of complex parasite communities.

(2) The helminth community of lesser scaup is a mature one, with a long evolutionary history.

LITERATURE CITED

Allan, J.D. 1975. Components of diversity. Oecologia 18:359-367.

Archer, D.M. and C.A. Hopkins. 1958. Studies on cestode metabolism. V. The chemical composition of *Diphyllobothrium* sp. in the pleurocercoid and adult stages. Exp. Parasit. 7:452-554.

Avery, R.A. 1969. The ecology of tapeworm parasites in wildfowl. Wildfowl 20:59-69.

Bakke, T.A. 1972. Studies on the helminth fauna of Norway XXII: The common gull, *Larus canus* L., as final host for digenea (platyhelminthes). I. The ecology of the common gull and the infection in relation to season and the gulls' habitat, together with distribution of the parasites in the intestine.

Barr, A. J. and J.H. Goodnight. 1972. A user's guide to the Statistical Analysis System. Students Supply Stores, N.C. State Univ., Raleigh, N.C.

Baer. J.G. 1971. Animal parasites. McGraw-Hill, N.Y.

Bethel, W.M. 1972. Altered behaviour leading to selective predation of amphipods infected with acanthocephalans, with special reference to *Polymorphus paradoxus*. Ph. D. thesis, Univ. of Alberta, Edmonton.

Buscher, H.N. 1965. Dynamics of the intestinal helminth fauna of three species of ducks. J. Wildl. Manage. 29:772-781.

Cannon, L.R.G. 1972. Studies on the ecology of the papillose allocreadiid trematodes of the yellow perch in Algonquin Park, Ontario. Can. J. Zool. 50:1231-1239.

Carmichael, J.W. and P.H.A. Sneath. 1969. Taxometric maps. Syst. Zool. 18:402-415.

Chandler, A.C. 1939. The effects of number and age of worms on development of primary and secondary infections with *Hymenolepis diminuta* in rats and an investigation into the true nature of "premunition" in tapeworm infection. Am. J. Hyg. 29:105-114.

Chubb, J.C. 1962. Acetic acid as a diluent and dehydrant in the preparation of whole, stained helminths. Stain Technol. 37:179-182.

Colbo, M.H. 1965. Taxonomy and ecology of the helminths of the American coot in Alberta. M.Sc. thesis, University of Alberta, Edmonton.

Cornwell, G.W. and A.B. Cowan. 1963. Helminth populations of the canvasback (*Aythya valisineria*) and host-parasite-environmental interrelationships. Tr. N. Amer. Wild. and Nat. Res. Conf. 28: 173-198.

Crofton, H.D. 1963. Nematode parasite populations in sheep and on pasture. Commonw. Bur. Helminthol. Tech. Commun. No. 35.

Crompton, D.W.T. 1970. An ecological approach to acanthocephalan physiology. Camb. Monogr. Exp. Biol. 17. Cambridge Univ. Press.

_____. 1973. The sites occupied by some parasitic helminths in the alimentary tract of vertebrates. Biol. Rev. 48:27-83.

Crompton, D.W.T. and J.G. Harrison. 1965. Observations on *Polymorphus minutus* (Goeze, 1782) (Acanthocephala) from a wildfowl reserve in Kent. Parasitology. 55:345-355.

Culver, D.C. 1972. A niche analysis of Colorado ants. Ecology 53:126-131.

Czaplinski, B. 1956. Hymenolepididae Fuhrmann, 1907 (Cestoda) parasites of some domestic and wild Anseriformes in Poland. Acta. Parasit. Pol. 4:175-373.

_____. 1973. Fauna and ecology of Hymenolepididae parasitizing wild mute swans in Poland. Mat. Internatl. Conf. on Hymenol., Warsaw. pp. 15-32.

Denny, M. 1969. Life cycles of helminth parasites using *Gammarus lacustris* as an intermediate host in a Canadian Lake. Parasitology 59:795-827.

Dudzinski, M.L. and R. Myktowycz. 1963. Relationship between sex and age of rabbits, *Oryctolagus cuniculus* (L.) and infection with nematodes *Trichostrongylus retortaeformis* and *Graphidium strigosum*. J. Parasit. 49:55-59.

Eichler, W. 1966. Two new evolutionary terms for speciation in parasitic animals. Syst. Zool. 15: 216-218.

Fager, E.W. 1957. Determination and analysis of recurrent groups. Ecology 38:586-95.

Goodchild, C.G. and O.C. Wells. 1957. Amino acids in larval and adult tapeworms (*Hymenolepis diminuta*) and in the tissues of their rat and beetle hosts. Exp. Parasit. 6:575-585.

Graham, L.C. 1966. The ecology of helminths in breeding populations of lesser scaup (*Aythya affinis*) and ruddy ducks (*Oxyura jamaicensis*). M.Sc. thesis, Univ. of Alberta, Edmonton.

Hair, J.D. and J.C. Holmes. 1975. The usefulness of measures of diversity, niche width and niche overlap in the analysis of helminth communities in waterfowl. Acta Parasit. Pol. 23:59-75.

Hill, M.O. 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54:427-432.

Holmes, J.C. 1961. Effects of concurrent infections on *Hymenolepis diminuta* (Cestoda) and *Moniliformis dubius* (Acanthocephala). I. General effects and comparison with crowding. J. Parasit. 47:209-216.

_____. 1973. Site selection by parasitic helminths: interspecific interactions, site segregation, and their importance to the development of helminth communities. Can. J. Zool. 51:333-347.

Holmes, J.C. and R.B. Podesta. 1968. The helminths of wolves and coyotes from the forested regions of Alberta. Can. J. Zool. 46:1193-1204.

Hutchinson, W.M. 1957. The incidence and distribution of *Hydatigena taeniaeformis* and other intestinal helminths in Scottish cats. J. Parasit. 43:318-321.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? Amer. Nat. 93:145-159.

Inglis, W.G. 1971. Speciation in parasitic nematodes. Adv. Parasit. 9:185-223.

Jarecka, L. 1958. Plankton crustaceans in the life cycles of tapeworms occurring in Druzno Lake. Acta Parasit. Pol. 6:63-108.

_____. 1961. Morphological adaptations of tapeworms eggs and their importance in the life cycles. Acta Parasit. Pol. 9:409-426.

Keast, A. 1968. Competitive interactions and the evolution of ecological niches as illustrated by the Australian honeyeater genus *Melithreptus* (Meliphagidae). Evolution 22:762-784.

Kerekes, J. 1965. Comparative limnological study of five lakes in central Alberta. M.Sc. thesis, Univ. of Alberta, Edmonton.

Krebes, C.J. 1972. Ecology: The experimental analysis of distribution and abundance. Harper and Row Publ. N.Y.

Lewis, J. 1966. An ecological analysis of the helminth fauna of some British small mammals. Proc. First Int. Congr. Parasit. 1:487-488.

MacArthur, R.H. 1960. On the relative abundance of species. Amer. Nat. 94:25-34.

McDonald, M.E. 1969. Catalogue of helminths of waterfowl (Anatidae). U.S. Dept. Int. Spec. Scient. Rpt. - Wild. No. 126.

Macfadyen, A. 1964. Animal ecology aims and methods. Sir Issac Pitman and Sons Ltd., London.

Mackenzie, K. and D. Gibson. 1970. Ecological studies of some parasites of plaice, *Pleuronectes platessa* and flounder, *Platichthys flesus*. In: Aspects of Fish Parasitology. Blackwell Sci. Publ. Oxford.

McLaughlin, J.D. and M.D.B. Burt. 1973. Changes in the cestode fauna of the black duck, *Anas rubripes* (Brewster). Can. J. Zool. 51: 1001-1006.

Mettrick, D.F. and C.E. Cannon. 1970. Changes in the chemical composition of *Hymenolepis diminuta* (Cestoda: Cyclophylidea) during prepatent development within the rat intestine. Parasitology 61:229-243.

Mettrick, D.F. and R.B. Podesta. 1975. Ecological and physiological aspects of helminth-host interactions in the mammalian gastrointestinal canal. Adv. Parasit. 12:183-249.

Miller, R.B. 1943. Studies on cestodes of the genus *Triaenophorus* from fish of Lesser Slave Lake, Alberta. I. Introduction and the life of *Triaenophorus crassus* and *T. nodulosus* in the definitive host, *Esox lucius*. Can. J. Res. 21:160-170.

_____. 1952. A review of the *Triaenophorus* problem in Canadian lakes. Fish. Res. Bd. Can. Bull. No. 95.

Neraasen, T.G. 1970. Ecology of the helminths of three species of arctic-nesting geese with particular reference to the lesser snow goose (*Chen caerulescens caerulescens*): A community analysis. M. Sc. thesis, University of Alberta.

Nilsson, N.A. 1967. Interactive segregation between fish species. *in* S.D. Gerking, ed. The biological basis of freshwater fish production. Blackwell Sci. Publ., Oxford.

Olszewska, G. 1973. Topospecificity of three species of the genus *Diorchis* parasitizing *Fulica atra* (L.). Mat. Internatl. Conf. on Hymenol., Warsaw. pp. 97-101.

Peet, R.K. 1974. The measurement of species diversity. Ann. Rev. Ecol. and Syst. 5:285-307.

Petter, A.J. 1962. Redescription et analyse critique de quelques especes d'Oxyures de la Tortue grecque (*Testudo graeca* L.). Diversite des structures cephaliques (II). Ann. Parasit. Hum. Comp. 37:140-152.

_____. 1966. Equilibre des especes dans les populations de nematodes parasites du colon des tortues terrestres. Mem. Mus. Natl. Hist. Nat. Paris Ser. A. Zool. 39(1): 1-252.

Pielou, E.C. 1969. An introduction to mathematical ecology. Wiley-Interscience, N.Y.

Podesta, R.B. and J.C. Holmes. 1970. Hymenolepidid cysticercoids in *Hyalella azteca* of Cooking Lake, Alberta: Life cycles and descriptions of four new species. J. Parasitol. 56:1124-1134.

Reichenow, E., H. Vogel and F. Weyer. 1952. Leitfaden zur Untersuchung der tierischen Parasiten des Menshchen und der Haustiere. Third ed. Leipzig.

Schad, G.A. 1962. Studies on the genus *Kalicephalus* (Nematoda: Diaphanocephalidae). II. A taxonomic revision of the genus *Kalicephalus* Molin, 1861. Can. J. Zool. 40:1035-1165.

1963. Niche diversification in a parasite species flock. Nature 198:404-406.

Schiller, E.L. 1951. *Hymenolepis hopkinsi*, n. sp., a cestode from the Black Duck. Amer. Midl. Nat. 45:253-256.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Shannon, C.E. and W. Weaver. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana, Ill.

Simpson, E.H. 1949. Measurement of diversity. Nature 163:688.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry, the principles and practice of statistics in biological research, W.H. Freeman and Co., San Francisco.

Spasskaya, L.P. 1966. Cestodes of birds of the U.S.S.R. Hymenolepididae. [In Russian]. Izdat. "Nauka", AN S.S.S.R., AN Moldav. S.S.R., Inst. Zool., Moskva. 698 pp.

Steel, R.G.D. and J.H. Torrie. 1960. Principles and procedures of statistics, with special reference to the biological sciences. McGraw-Hill Co., Inc., Toronto.

Stradowski, M. 1973a. Characteristics of populations of *Diorchis stefanskii* (Czaplinski 1956) in experimentally infected domestic ducks. Mat. Internatl. Conf. on Hymenol., Warsaw. pp. 115-118.

_____. 1973b. A study of *Diorchis stefanskii* (Czaplinski, 1956) populations (Cestoda: Hymenolepididae) in experimentally infected domestic ducks. Acta Parasit. Pol. 21:349-357.

Sugden, L.G. 1973. Feeding ecology of pintail, gadwall, American widgeon and lesser scaup ducklings. Can. Wildl. Serv. Report Ser. No. 24, Ottawa.

Sulgostowska, T. 1958. Flukes of birds of Druzno Lake. (Parasitofauna of the biocoenosis of Druzno Lake - Part III). Acta Parasit. Pol. 6:111-142.

Terborgh, J. 1971. Distribution on environmental gradients: Theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. Ecology 25:23-40.

Uglem, G.L. and S.M. Beck. 1972. Habitat specificity and correlated aminopeptidase activity in the acanthocephalans *Neoechinorhynchus cristatus* and *N. crassus*. J. Parasit. 58:911-920.

Ulmer, M.J. 1971. Site-finding behaviour in helminths in intermediate and definitive hosts. *in* M. Fallis, ed. Ecology and physiology of parasites. Univ. Toronto Press, Toronto.

Valkounova, J. 1973. Reservoir parasitism in cestodes of the family Hymenolepididae (Ariola, 1899) parasitic in domestic and wild ducks. Vest. Cesk. SPol. Zool. 37:71-75.

Wehr, E.E. and C.M. Herman. 1954. Age as a factor in the acquisition of parasites by Canada geese. J. Wildl. Manage. 18:239-247.

Wertheim, G. 1970. Experimental concurrent infections with *Strongyloides ratti* and *S. venezuelensis* in laboratory rats. Parasitology 61:389-395.

Whittaker, R.H. 1965. Dominance and diversity in land plant communities. Science 147:250-260.

Whittaker, R.H., S.A. Levin and R.B. Root. 1973. Niche, habitat and ecotope. Amer. Nat. 107:321-338.

Wisniewski, W.L., K. Szymanik and K. Bazanska. 1958. The formation of a structure in tapeworm populations. Cesk. Parasit. 5:195-212.

Appendix I. Life history data for local populations of the dominant helminths of lesser scaup.

Helminths	Intermediate Hosts*	Definitive Hosts		Development Time (Days)	
		Main	Auxilliary	Intermediate Host	Prepatent Period
Cestoda					
Dicranotaenia coronula	unknown locally, variety of crustaceans elsewhere[6]	Various dabbling and diving ducks[2,4,5]		–	–
Fimbriaria fasciolaris	*Gammarus lacustris*[1] *Hyalella azteca*[3]	Various dabbling and diving ducks[1,2,3,4,5]		13[1], 7[3]	11[1], 5[3]
Hymenolepis abortiva	unknown locally, *Gammarus pulex* elsewhere[6]	Lesser scaup[4]		–	–
H. albertensis	*G. lacustris*[1]	White-winged scoters[1,3]	Lesser scaup ducklings[4]	8[1]	6[1]
H. fausti	unknown locally, variety of crustaceans elsewhere[6]	?	Lesser scaup[4]	–	–
H. microskrjabini	*G. lacustris*[1]	Lesser scaup[1,4]		8[1]	6[1]
H. pusilla	*H. azteca*[3]	Lesser scaup[3,4]	Canvasback[3]	9[3]	14[3]
H. recurvata	–	Lesser scaup[4]		–	–
H. spinocirrosa	*H. azteca*[3]	Lesser scaup[4,5]		9[3]	4[3]
H. tuvensis	*G. lacustris*[1] *H. azteca*[1,3]	Lesser scaup[1,2,3,4,5]	Redheads, canvasbacks, white-winged scoters[3,5]	? 11[3]	7[1] 4[3]
Lateriporus skrjabini	*G. lacustris*[1]	Lesser scaup[1,2,3]	Redheads, canvasbacks[1,2]	36[1]	8[1]
Retinometra pittalugai	–	Lesser scaup[1,4]		–	–
Acanthocephala					
Polymorphus marilis	*G. lacustris*[1]	Lesser scaup[1,2,4,5]	Ruddy ducks[2] Redheads[1] Red-necked grebes[4]	34[1]	21[1]

*Authors: [1]Denny 1969; [2]Graham 1966; [3]Podesta and Holmes 1970; [4]this study; [5]unpublished records; [6]McDonald 1969.

Appendix II. Seasonal dynamics of the dominant species of helminths from 30 adult lesser scaup collected at Cooking and Hastings Lakes, Alberta, 1973-74.

Helminth Species	Year / Month / No. examined	1973 June 5	1973 July 5	1973 August 5	1974 June 5	1974 July 5	1974 August 5	ANOVA Season F	ANOVA Year F
Hymenolepis spinocirrosa	I	1523±1443(5)[a]	1349±521(5)	1506±676(5)	338±247(5)	191±137(4)	1000±395(5)		
	M	10119±5468(5)	4992±3645(5)	7208±4742(5)	3021±3107(5)	1860±1894(4)	11394±11007(5)		
	Σ	39	33	37	38	23	37	3.19*	1.17
H. abortiva	I	3732±3850(5)	1180±780(5)	2186±3682(5)	1052±925(5)	93±92(5)	871±776(4)		
	M	5470±3379(5)	3959±4120(5)	4446±4428(5)	2291±2507(5)	1252±936(4)	6836±6279(4)		
	Σ	31	27	30	37	15	33	1.18	.82
H. pusilla	I	255±106(2)	1487±715(5)	599±508(5)	749±913(4)	311±231(4)	613±619(5)		
	M	1292±2011(4)	4581±6727(4)	4679±5932(4)	428±644(4)	992±1636(4)	3338±3763(5)		
	Σ	4	27	18	11	14	21	.81	.54
H. microskrjabini	I	1201±2293(4)	367±412(4)	237 (1)	70±45(3)	101±102(3)	(0)		
	M	6499±12435(4)	489±734(4)	3904 (1)	84±72(3)	663±1137(3)	11 (1)		
	Σ	21	4	4	1	6	<1	.53	.09
H. tuvensis	I	428±223(2)	932±1682(4)	405±191(2)	101±72(5)	611±1010(4)	135±125(3)		
	M	757±380(4)	285±471(4)	453±493(4)	115±95(5)	2371±4339(4)	1419±1479(4)		
	Σ	3	5	2	3	33	7	.70	.11
Retinometra pittalugai	I	53±67(2)	381±237(5)	1541±2389(4)	920±1495(4)	30±50(4)	126±68(3)		
	M	409±580(3)	(0)	2179 (1)	463 (1)	43±77(4)	290 (1)		
	Σ	1	2	7	9	1	1	.83	1.10
Fimbriaria fasciolaris	I	59±66(5)	67±55(5)	696±476(5)	36±32(5)	74±129(5)	156±94(5)		
	M	12±13(4)	10 (1)	46±56(3)	9±7 (3)	16±20(4)	21±19(4)		
	Σ							7.17***	.79
H. recurvata	I	7±47(4)	61±83(2)	(0)	92 (1)	154±155(3)	(0)		
	M	20±269(5)	125 (1)	(0)	1 (1)	443±736(4)	(0)		
	Σ	<1	<1	0	<1	6	0	.16	.15
Polymorphus marilis	I	9 (1)	5±1(3)	31 (1)	(0)	2 (1)	(0)		
	M	11±9(5)	52±61(5)	72±61(5)	36±17(5)	25±18(5)	155±128(5)		
	Σ	<1	<1	<1	<1	<1	1	3.15*	.99
Lateriporus skrjabini	I	(0)	42±29(4)	7±8(3)	9 (1)	2±1(2)	2±3(4)		
	M	7 (1)	70±95(3)	31±46(4)	12±11(3)	11±11(2)	17±18(4)		
	Σ	<1	<1	<1	<1	<1	<1	1.77	.81
Dicranotaenia coronula	I	20±29(3)	(0)	27 (1)	5±5(3)	(0)	16±6(2)		
	M	11±13(2)	16 (1)	35±16(2)	(0)	26±30(2)	45±33(2)		
	Σ	<1	<1	<1	<1	<1	<1	1.71	.32

[a] I = mean (±SD) immature specimens/infected bird

M = mean (±SD) mature specimens/infected bird

Σ = percent of total monthly fauna

(n) = number infected

* $p<.05$

*** $p<.001$

Appendix III. Acquisition of the dominant species of helminths from 52 lesser scaup ducklings collected at Cooking and Hastings Lake, Alberta, late July, 1973-74.

Year	Host Age	No. Exam.		HELMINTH SPECIES: *Hymenolepis spinocirrosa*	*H. microskrjabini*	*H. tuvensis*	*H. pusilla*	*H. abortiva*	*H. albertensis*	*H. fausti*	*Fimbriaria fasciolaris*	*Lateriporus skrjabini*	*Polymorphus marilis*	*Dicranotaenia coronula*
1973	Ia	5	I	64±64(5)[1]	15±12(5)	14±13(5)	49±31(4)	9±1(2)	137±127(5)		79±57(5)	2±2(3)	1 (1)	3±.7(2)
			M	375±364(5)	88±72(5)	30±25(4)	(0)	30±27(2)	97±42(5)	(0)	10 (1)	3 (1)	1 (1)	(0)
			I	46	11	4	6	2	24		8	<1	<1	<1
	Ib	5	I	82±90(5)	8±4(3)	18±3(3)	30±27(5)	13±19(4)	49±50(4)	37 (1)	68±29(5)	(0)	1 (1)	2±2(4)
			M	677±373(5)	159±96(3)	60±24(4)	137±108(2)	51±31(4)	150±165(5)		58±37(4)	2 (1)	5±.7(2)	(0)
			I	55	7	4	6	4	14	<1	8	<1	<1	<1
	Ic	6	I	84±48(5)	27±46(4)	19±16(3)	38±43(4)	27±18(3)	20±14(3)		35±28(6)	1±0(2)	(0)	3±1(3)
			M	678±439(6)	270±245(6)	163±207(6)	158±122(6)	104±68(4)	198±185(6)	(0)	87±40(6)	3±2(4)	3±2(4)	3±2(3)
			I	40	18	9	10	5	11		7	<1	<1	<1
1973	IIa	5	I	165±118(4)	14±22(4)	27±27(3)	38±28(4)	40±38(2)	1 (1)		55±56(5)	2±3(4)	(0)	(0)
			M	1968±852(5)	374±271(5)	326±65(5)	262±65(5)	230±194(4)	48±29(4)	(0)	83±54(5)	10±7(4)	3±2(5)	4±4(3)
			I	58	11	10	8	6	1		4	<1	<1	<1
	IIb	6	I	255±384(5)	141±129(5)	58±55(5)	13±15(5)	79±76(2)	(0)		72±43(6)	3±4(3)	(0)	(0)
			M	1802±1817(6)	645±566(6)	634±422(6)	363±147(6)	444±242(5)	209±245(3)	2 (1)	29±21(6)	36±38(5)	6±4(6)	9±8(6)
			I	45	17	15	8	9	2	<1	2	1	<1	<1
1974	Ia	6	I	13±16(6)			6 (1)				1 (1)			
			M		(0)	(0)		(0)	(0)	(0)		(0)	(0)	(0)
			I	92			7				1			
	Ib	6	I	540±433(6)	15±23(4)	5 (1)	26±20(5)	28±19(4)	24±31(3)	2 (1)	26±9(6)	(0)	1 (1)	(0)
			M	975±948(6)	44±50(5)	4±4(2)	23±23(3)	65±60(5)	47±85(5)		(0)	(0)	1 (1)	(0)
			I	86	3	<1	2	4	3	<1				
	Ic	5	I	86±51(3)	35±44(5)	19±13(2)	65±21(2)	38±48(4)	34±9(2)		30±38(4)	1 (1)	(0)	(0)
			M	523±403(5)	568±955(5)	88±112(5)	115±95(4)	147±278(5)	178±18(2)	(0)	39 (1)	11±14(2)	8±9(4)	(0)
			I	34	35	6	7	11	5			<1		
1974	IIa	8	I	155±157(3)	11±13(2)	15±5(3)	21±14(2)	71±73(3)	17±11(2)	7 (1)	62±41(3)	2 (1)	(0)	2 (1)
			M	1107±515(3)	118±33(3)	174±131(3)	126±72(3)	164±155(3)	204±167(3)	77±107	38±22(3)	1 (1)	2±0(2)	2±1(2)
			I	54	5	8	6	10	10	<1		<1		<1
	IIb	5	I	74 (1)	0	10 (1)	22 (1)	20 (1)	42±45(2)	102±76(2)	22±27(4)	3 (1)	1 (1)	1 (1)
			M	761±782(3)	53±46(5)	100±7(2)	173±42(2)	369±426(2)	46±18(2)	1012±614(4)	49 (1)	4±4(2)	21±18(4)	17±6(3)
			I	27	5	3	4	9	2	48	1	<1	1	1
	IIb[2]	2	I	74 (1)	0	10 (1)	22 (1)	20 (1)	42±45(2)	48 (1)	17±35(2)	0	0	1 (1)
			M	1141±599(2)	102±0(2)	100±7(2)	173±42(2)	369±426(2)	46±18(2)	420 (1)	49 (1)	4±4(2)	4 (1)	0
			I	49	7	5	8	16	4	9	2	<1	<1	<1
ANOVA		Age(F)		13.21***	5.42*	21.04***	149.30***	25.[illegible]***	.93	.08	1.13	1.11		
		Year(F)		.79	.83	1.11	1.99		.07	5.11	.21	.44		

[1] I = mean (±SD) immature specimens/infected birds
M = mean (±SD) mature specimens/infected birds
I = percent of total cohort fauna
() = number infected

[2] = excluding birds with exceptionally high populations of *H. fausti*

\+ indicates significant linear regressions

* $p<.05$
*** $p<.001$

Appendix IV. Intraintestinal distribution of the dominant species of helminths from 30 adult lesser scaup compared with four alternative patterns of community organization (see text for application).

Helminth species	Group	n	N	Median Point	End Points of Distribution		Range
Fimbriaria fasciolaris	Total	30	194± 316	8± 4	0	19± 8	19± 8
	A	6	20± 16	8± 3	0	17± 7	17± 7
	B	5	135± 124	9± 6	0	20±10	20±10
	C	3	31± 26	6± 3	0	17±10	17±10
	D	12	393± 426	8± 3	0	22± 7	22± 7
Lateriporus skrjabini	Total	18/30	37± 51	19± 8	11± 9	28± 9	18±11
	A	4/6	9± 9	23± 9	16± 9	26± 9	10± 0
	B	4/5	49± 36	20± 9	5± 4	26±10	21± 8
	C	0/6	-	-	-	-	-
	D	7/12	37± 48	17± 7	9± 9	26± 8	17±13
Hymenolepis recurvata	Total	12/30	320± 521	24±11	10± 9	36±14	27±17
	A	2/6	49± 62	30±11	23± 1	33± 4	10± 0
	B	2/5	180± 238	8± 7	0	20±21	20±21
	C	3	788± 926	28± 9	3± 3	40±10	37±10
	D	3/12	110± 124	33± 5	12±12	45±18	33±28
H. microskrjabini	Total	17/30	2419±7145	27±11	15±12	40±11	25±15
	A	6	53± 18	30± 7	19±11	38± 3	19±11
	B	5	1687±1540	21± 6	5± 4	39± 7	34±10
	C	2/3	106± 112	33± 0	30± 0	38± 4	8± 4
	D	1/12	45	13	5	20	15
Retinometra pittalugai	Total	23/30	715±1616	40±11	27±14	54±15	27±22
	A	5/6	790±1576	53± 4	36±12	64±12	13±12
	B	4/5	151± 252	40± 9	30±16	51±19	21±29
	C	3/3	163± 88	41± 3	35± 0	52±10	17±10
	D	9/12	1200±2303	38±10	19±10	57±15	38±21
H. spinocirrosa	Total	29/30	7609±6806	37±14	18±13	58± 9	39±14
	A	6	1699±1574	49± 6	31± 6	64±13	33±13
	B	5	4640±2735	38± 9	23±10	56± 7	33±10
	C	3	5290±5065	51± 6	35± 5	63± 8	28± 8
	D	12	12033±6434	35±11	8± 7	57± 5	48± 8
H. tuvensis	Total	25/30	1218±2316	48± 8	35±10	61±11	25±14
	A	5/6	89± 81	48± 9	29±20	60± 9	25± 9
	B	5	2572±4711	44± 4	28± 9	60±13	32±17
	C	3	1115± 665	54± 3	37± 8	62± 8	25± 5
	D	9/12	702±1067	49± 9	39± 8	58±12	19±13
H. abortiva	Total	29/30	5077±5254	64± 8	51± 6	84± 9	30±13
	A	6	1928± 989	65± 4	53± 5	84± 8	31±12
	B	5	5721±4406	59± 4	46± 2	80±11	34±10
	C	3	2313±2187	68± 0	57± 3	87± 8	30±10
	D	12	7131±6547	62± 7	50± 6	82± 9	33±12

Appendix IV (continued)

Helminth species	Group	n	N	Median Point	End Points of Distribution		Range
Polymorphus marilis	Total	30	60± 76	66± 6	51± 8	85± 8	33±12
	A	6	29± 19	68± 8	51± 9	88± 8	37± 5
	B	5	50± 48	67± 7	52± 5	83±10	31±11
	C	3	15± 15	68± 0	57± 3	75± 0	18± 3
	D	12	93± 103	65± 7	49± 9	85± 7	35±13
Dicranotaenia coronula	Total	14/30	27± 27	73±21	70±10	89±11	18±10
	A	1/6	10	68	65	70	5
	B	3/5	2± 2	80±11	75±10	88± 8	13± 8
	C	2/3	34± 18	78± 7	70± 7	93±11	23± 4
	D	7/12	41± 28	82±11	70±12	92±10	22±12
H. pusilla	Total	28/30	2871±4081	90± 4	76± 7	99± 1	22± 9
	A	6	758± 715	88± 5	79± 7	98± 4	18± 7
	B	5	2321±1884	87± 2	71± 7	100± 0	29± 7
	C	3	519± 307	91± 8	80± 5	100± 0	20± 5
	D	11/12	4367±4272	90± 3	77± 6	100± 0	23± 6